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Intra-tooth variations in $\delta^{18}O$ (PO_4) of mammalian tooth enamel as a record of seasonal variations in continental climate variables

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ABSTRACT—Regular intra-tooth variations in the $\delta^{18}O$ value of mammalian tooth enamel phosphate ($\delta^{18}O_p$) have been considered a potential measure of seasonal changes in continental climate variables since they were first observed. In order to investigate this possibility in more detail, analyses were made of teeth from a number of mammalian herbivores (sheep, cattle, elk, and pigs) that lived over a wide range of geographic locations, ecological settings, and climatic conditions (Iowa, Florida, Wyoming, Iceland, England, Croatia, and the Philippines). The lack of intra-tooth $\delta^{18}O_p$ variations in teeth of cattle that were given tap water to drink provides strong evidence that the underlying cause of observed intra-tooth variations is primarily a change in the isotopic composition of ingested water. In concert with this interpretation, the range of intra-tooth $\delta^{18}O_p$ values and their absolute values from each locality mirror observed differences in the range and absolute $\delta^{18}O$ values of local precipitation ($\delta^{18}O_{pt}$) and in climate variables. Thus intra-tooth $\delta^{18}O_p$ values can indeed be considered a qualitative measure of seasonal climate change in continental settings. Quantitative use of intra-tooth $\delta^{18}O_p$ values as a climate proxy is possible, but is hindered by lack of detailed information on aspects of mammalian physiology, behavior, and perhaps local hydrology that may also play a role in influencing $\delta^{18}O_p$. This problem is exemplified by the different range in $\delta^{18}O_p$ values measured for sheep and cattle from the same locality around York, UK (3.4 vs. 2.6‰, respectively). The observed difference most likely reflects a difference in the relative amount of leaf water ingested by the two species. Future studies of well-constrained samples are required to test physiological models and to develop empirical relations that accurately relate $\delta^{18}O_p$ to $\delta^{18}O_{pt}$. In addition to their use as indicators of seasonality, intra-tooth variations in $\delta^{18}O_p$ values provide valuable information for longer-term climate change and paleobiological investigations. *Copyright © 1998 Elsevier Science Ltd*

1. INTRODUCTION

In order to describe fully the nature of past climatic conditions in continental environments, it is necessary to have some measure of the extent to which variables such as temperature and amount of precipitation varied over the course of a year (i.e., seasonality). Both variables reflect the movement of heat and moisture from source to sink regions and in addition play a primary role in determining the spatial distribution of different plants and animals and hence the ecological development of a given area. The greatest hindrance to studying such short-term climate variations in the past has been finding a proxy for them that has seasonal resolution, that has the potential to be preserved over millions of years, and that is relatively common. Recent investigations of oxygen isotope variations of phosphate in mammalian tooth enamel ($\delta^{18}O_p$), however, indicate that regular intra-tooth variations in $\delta^{18}O_p$ values (e.g., Fricke and O'Neil, 1996; Kohn et al., 1998; Stuart-Williams and Schwarcz, 1997) may provide just such a proxy for seasonal variations in continental climate variables over geologic time. Similar variations also occur in $\delta^{18}O$ values of carbonate in mammalian teeth (Koch et al., 1989; Fricke et al., 1998), but carbonate is more likely than phosphate to undergo isotopic alteration in diagenetic environments (Kolodny et al., 1983; Shemesh et al., 1988; Fricke et al., 1998).

There are three main reasons why it should be possible to use intra-tooth $\delta^{18}O_p$ values as a proxy for climate variables on a seasonal time scale. First, there are good correlations between oxygen isotope compositions of precipitation ($\delta^{18}O_{pt}$) and continental climate variables. In mid-to high-latitude continental areas, there is a strong positive correlation between $\delta^{18}O_{pt}$ and temperature (lower and higher values are associated with colder and warmer temperatures, respectively), and there is a slightly weaker negative correlation between $\delta^{18}O_{pt}$ and the amount of precipitation in tropical island stations (lower and higher values are associated with more and less precipitation, respectively; Dansgaard, 1964; Yurtsever and Gat, 1981; Rozanski et al., 1993). Second, local surface waters constitute the primary source of oxygen in the body water of a mammal. Both empirical evidence and theoretical considerations suggest that $\delta^{18}O_p$ values of hydroxyapatite in enamel from large (>1 kg) animals mirror $\delta^{18}O$ values of local precipitation ingested from surface reserviors such as streams, ponds, and plants (e.g., Longinelli, 1984; Luz et al., 1984; Luz and Kolodny, 1985; Bryant and Froelich, 1995; Kohn, 1996). Leaf water, however, can be modified isotopically relative to precipitation due to evaporation at the leaf surface (e.g., Flanagan et al., 1991). Lastly, mammalian tooth enamel precipitates in isotopic equilibrium with body water at a relatively constant temperature of ~37°C (Longinelli, 1984; Luz et al., 1984) and forms incrementally from the crown to the base of the tooth as it erupts. Enamel, therefore, preserves a time series of $\delta^{18}O_p$ values

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along the direction of growth that reflect only changes in $\delta^{18}O$ of ingested water, and thus presumably climate variables.

This study was undertaken in an effort to confirm that intra-tooth variations in $\delta^{18}O_p$ of mammalian tooth enamel can be used as a proxy for seasonality. Teeth from cattle that drank only ground water (isotopically homogeneous through time) were analyzed in order to evaluate intra-tooth variations in $\delta^{18}O_p$ values that might occur independently of changes in the $\delta^{18}O$ value of ingested water. Intra-tooth samples of teeth from different mammalian species that lived in several climatologically diverse localities were then analyzed in order to check for possible covariation between seasonal ranges in $\delta^{18}O_p$, $\delta^{18}O_{pt}$, temperature, and amount of precipitation.

2. OXYGEN IN BIOGENIC PHOSPHATE

Although $\delta^{18}O$ values of biogenic phosphate often mirror $\delta^{18}O$ values of local precipitation, the relation between the two is not one to one. In general such relations have the form:

$$\delta^{18}O_p = m * \delta^{18}O_{pt} + c \qquad (1)$$

where the slope m has a value between 0.6 and 0.8 depending on the species in question (see references in Bryant and Froelich, 1995). Slopes of less than unity arise because mammalian body water, from which biogenic phosphate precipitates, has more positive $\delta^{18}O$ values than those of local precipitation as a result of metabolism and behavior particular to the species (e.g., Luz et al., 1984; Ayliffe and Chivas, 1990; Luz et al., 1990; Bryant and Froelich, 1995; Kohn, 1996; Stuart-Williams and Schwarcz, 1997). One of the most important agents of isotopic modification is atmospheric oxygen, which is used by a mammal during respiration and metabolism. This oxygen has a constant $\delta^{18}O$ value, and physiological models suggest that it accounts for ~25% of the oxygen flux into the body for most large mammals (Bryant and Froelich, 1995; Kohn, 1996). Fractionations associated with respiratory CO_2 and H_2O and heat loss processes such as sweating also result in an isotopic modification of mammalian body water (e.g., Bryant and Froelich, 1995; Kohn, 1996).

The $\delta^{18}O$ value of mammalian body water can also be affected by dietary behavior as well as physiological processes. Water from plant stems will have $\delta^{18}O$ values close to that of soil water (Yakir, 1992) , while leaf water has a higher $\delta^{18}O$ value as a result of evaporation at the leaf surface (e.g., Flanagan et al., 1991). In addition, the magnitude of this evaporative effect will vary depending on the local relative humidity and on the particular photosynthetic pathway utilized by local plants (e.g., Sternberg et al., 1984). The influence of leaf water, and hence relative humidity, on $\delta^{18}O_p$ values has been demonstrated for several herbivore species (e.g., Ayliffe and Chivas, 1990; Luz et al., 1990). In addition, oxygen bound in organic matter can influence $\delta^{18}O_p$ to a small degree (Bryant and Froelich, 1995; Kohn, 1996; Blake et al., 1997), and its $\delta^{18}O$ is ~27‰ higher than that of leaf water from which it forms (e.g., Sternberg et al., 1989).

Both physiological models and empirical relations can be used to account for these physiological and behavioral modifications of $\delta^{18}O_p$ relative to $\delta^{18}O_{pt}$ (e.g., Ayliffe and Chivas, 1990; Luz et al., 1990; Bryant and Froelich, 1995; Kohn, 1996). An additional goal of this study was to identify the avenues of research that should be investigated in the future so that intra-tooth variations can be used as a quantitative climate proxy.

2. DESCRIPTION OF SAMPLES

2.1. Location

Analyses were made of teeth of mammalian herbivores from a number of localities described in Table 1. Herbivore teeth were chosen because they tend to be the most common in the fossil and archaeological record and because these high-crowned teeth are generally large enough to facilitate easy intra-tooth sampling. Only third molars and canine teeth were sampled in order to reduce possible effects of preweaning water sources on the isotopic compostion of the enamel analyzed (e.g., Bryant et al., 1996; Fricke and O'Neil, 1996). Because of the difficulty in securing teeth from a single species that lives over a wide geographic range, samples from several species were collected for analysis. It was possible, however, to stay within the order of Artiodactyla, which includes suids (pigs), cervids (elk), and bovids (cattle, sheep). In several cases teeth from two or more species from a single locality were available, and this overlap provided a check when comparing data from different taxa and locations.

The sampled teeth come from a variety of climatological and ecological regimes. The climatological regimes are described by the seasonal range and mean annual values of temperature, rainfall, and humidity. These data, collected from weather stations nearest to the sample localities, are presented in Table 1. The ecological conditions are quite variable, including living environments of wild and free-ranging domesticated animals from Teton County, Wyoming (elk, cattle), Croatia (elk), and the Philippines (pig), those of domesticated animals from southeastern Greenland, northern Iceland, England, and northern Florida (sheep and cattle), and the controlled environment of several cattle from an ongoing medical research project at the University of Iowa. With the exception of the samples from the north Atlantic region, all teeth were from individuals that died within the last 20 years. The north Atlantic material was collected from archaeological deposits ranging in age from 1000 to 400 yr B.P. (Addyman, 1990). Therefore, the intra-tooth variations in $\delta^{18}O_p$ recorded in these teeth do not represent climatic conditions that prevailed during the present century. Given the similarity in the range of intra-tooth $\delta^{18}O_p$ values from these archaeological deposits (see below), and the relatively stable nature of seasonal differences in $\delta^{18}O_{pt}$ values during the Holocene in general (e.g., Stuiver et al., 1995), it is valid to include the archaeological samples in this study of modern material.

In the case of the wild and free-ranging animals, the specific dietary and drinking habits of the individuals are not known, but it can be assumed that all of their ingested water came from plants and other small surface water reserviors, and hence mirrors local precipitation to a large degree. Domesticated animals from Greenland and Iceland were left to graze whenever snowcover was minimal (Thorsteinsson, 1985), and husbandry practices were likely to have been similar in York during the same time period (T. O'Conner, pers. commun.). Therefore, despite the human influence on their behavior, these animals probably acquired most of their water from free surface and plant reserviors, and we are assuming that such influence

Table 1. Summary of climate and $\delta^{18}O_{pt}$ data from the different sampled localities. MAT = mean annual temperature, and MAAP = mean annual amount of precipitation. Seasonal ranges (Δ) in temperature, amount of precipitation, relative humidity, and $\delta^{18}O_{pt}$ are presented by comparing average winter and summer endmembers. Endmember values are in turn determined by comparing the average monthly means of January and February (winter) with the average monthly means of July and August (summer). Endmember values and the range in $\delta^{18}O_{pt}$ for each locality is either taken from (1) the closest IAEA weather station, which is given in parentheses, or (2) it is estimated by using the isotopic contour map of Yurtsever and GAT (1981) to determine the mean annual $\delta^{18}O_{pt}$ value and Fig. 2 to estimate the range of $\delta^{18}O_{pt}$ values around this mean. Non-IAEA climate data from Landsberg (1985) and Gale Research Company (1985).

Location	Weather Station	MAT (°C)	Temp. (°C) Wint. to Sum.	MAAP (mm)	Precip. (mm) Wint. to Sum.	Rel. Humidity (%) Wint. to Sum.	Est. $\delta^{18}O_{pt}$ (‰) Wint. to Sum.
Teton County, WY	Bondurant	0.7	-12.5 to 13.7 $\Delta = 26.2$	477	119 to 57 $\Delta = 62$	56 to 26^^	-21.4 to -13.8
North Iceland	Akureyi	3.9	-1.6 to 10.6 $\Delta = 11.0$	474	43 to 37 $\Delta = 6$	79 to 70	-8.5 to -6.5
York, England	Waddington	9.4	3.3 to 16.2 $\Delta = 12.9$	600	48 to 60 $\Delta = 12$	89 to 79	-8.7 to -5.6 (Keyworth*)
Groennedal, Greenland	Groennedal	1.2	-4.4 to 7.7 $\Delta = 12.3$	1018	89 to 77 $\Delta = 12$	72 to 56	-13.5 to -11.5 (Groennedal*)
North Croatia	Zagreb	11.0	1.7 to 20.9 $\Delta = 19.2$	840	51 to 81 $\Delta = 30$	73 to 60	-12.0 to -6.3 (Zagreb*)
Luzon Is., Philippines	Tuguegarao	26.6	25.4 to 25.8 $\Delta = 0.4$	1763	30 to 253 $\Delta = 223$	84 to 76	-6.2 to -2.9
Alachua County, FL	Gainsville	27.4	20.6 to 33.1 $\Delta = 12.5$	1162	79 to 165 $\Delta = 86$	72 to 79‡	-3.6 to -3.5 (Tampa Bay*)
Ames, IA	Des Moines	15.2	-1.1 to 29.5 $\Delta = 30.6$	678	26 to 80 $\Delta = 54$	71 to 68	-9.4 to -5.8

^^RH data from Lander *IAEA station
‡RH data from Orlando

on these domesticated animals did not alter the natural dietary differences between sheep and cattle. The drinking habits of the Florida cattle are not as well constrained because these animals may have been given tap/groundwater in addition to water from natural surface reservoirs. In contrast, the cattle from Iowa were raised under controlled laboratory conditions in Ames, and they were given tap water to drink. Except for a small amount of summer graze, their diet was almost exclusively dry pellets of grain and hay that were grown in various Iowa locations.

2.2. Seasonal Range in $\delta^{18}O_{pt}$ Values

Because $\delta^{18}O_p$ provides a link to $\delta^{18}O_{pt}$ and thus to the climate variables temperature and amount of precipitation, it is necessary to know how $\delta^{18}O_{pt}$ values vary over the course of the year at each locality where samples were collected (Table 1). In some cases it is possible to use oxygen isotope data collected from nearby weather stations. York has a nearby station operated by the British Geological Survey (Talbot and Darling, 1997), while climatological and $\delta^{18}O_{pt}$ data for Croatia and Greenland come from weather stations operated by the International Atomic Energy Agency (IAEA, 1969–1994). At the other localities, the range in $\delta^{18}O_{pt}$ values was estimated using the global correlations between seasonal differences in temperature/amount of precipitation and seasonal differences in $\delta^{18}O_{pt}$ values (Fig. 1). The mean annual $\delta^{18}O_{pt}$ value for this range was in turn estimated from the isotopic contour map of Yurtsever and Gat (1981). It should be noted that the range in $\delta^{18}O_{pt}$ values estimated in this manner have an associated error of several permil, as is noted in Fig. 1.

3. ANALYTICAL METHODS

Multiple samples of ~6 mg of enamel from each tooth were drilled in horizontal bands parallel to the cervical margin and along the growth axis of each tooth for oxygen isotope analysis of phosphate, thus providing a time-series of $\delta^{18}O_p$ values over the period of enamel formation (Fig. 2). The analyses were made using the technique of O'Neil et al. (1994). After a series of simple chemical steps, the phosphate radical is isolated as Ag_3PO_4, which in turn is reacted with graphite in silica-glass tubes at 1400°C to form CO_2, which is then introduced to the inlet system of a mass spectrometer. Using this technique we obtain a value of 21.8 ± 0.3‰ (2σ) for NBS-120c, which is comparable to the values obtained using the conventional fluorination method, and a value of 12.1‰ ± 0.3‰ for our in-house UMS-1 standard.

4. RESULTS

The isotopic analyses are given in Table 2, and the intra-tooth variations in $\delta^{18}O_p$ for teeth from each locality are plotted in Fig. 3. These figures were constructed by plotting the $\delta^{18}O_p$ value of each sample as a function of relative position on the tooth (Figs. 1 and 3). In most cases, this position is determined by the absolute distance of the sample from the cervical margin of the tooth. There are instances, however, where the intra-tooth $\delta^{18}O_p$ values for different teeth from the same locality are out of phase with respect to their absolute position relative to

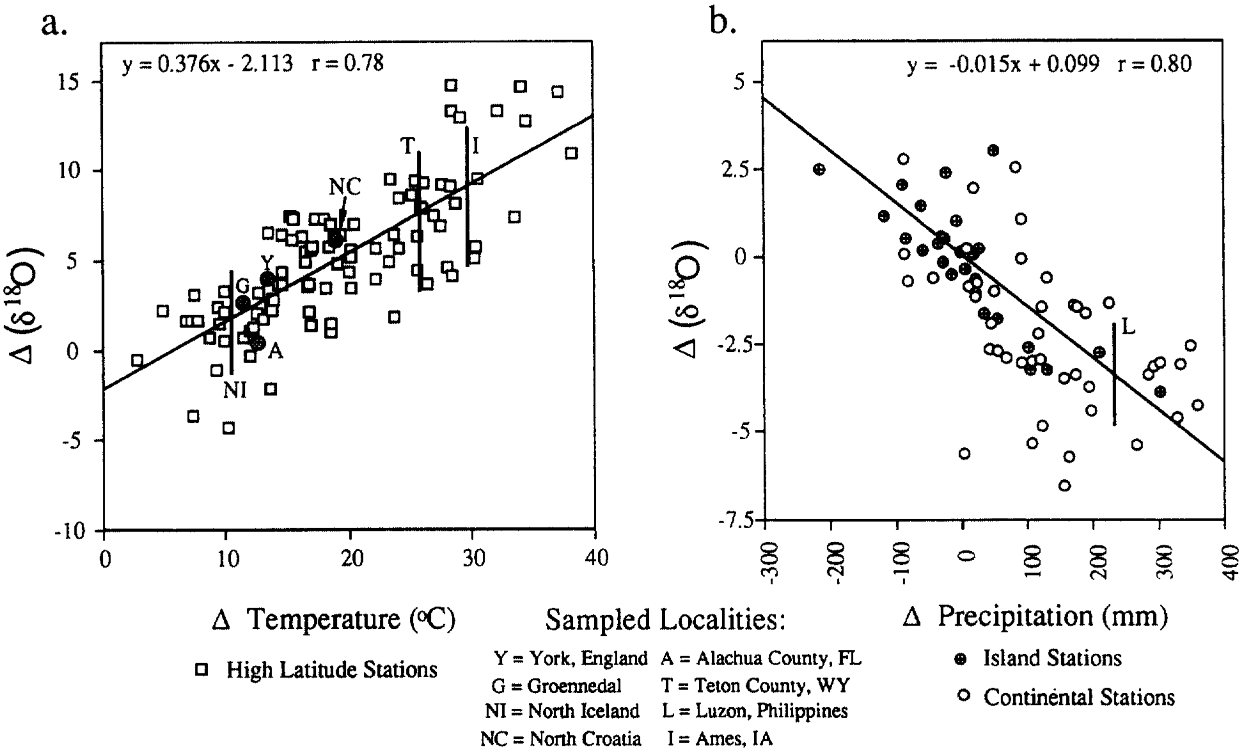

Fig. 1. Global correlations between seasonal differences in temperature, the amount of precipitation, and $\delta^{18}O_p$ (‰). In part (a), the seasonal range in temperature is plotted against the seasonal range in $\delta^{18}O_{pt}$ values for weather stations in the IAEA/WMO network located in the mid- to high-latitudes (IAEA, 1969–1994). Data from the few continental stations that are affected by the Asian monsoon are not included. The range is determined by taking the difference in average values for June, July, and August and average values for December, January, and February. Filled circles represent locations where the seasonal range in $\delta^{18}O_{pt}$ values are known from one of the IAEA stations, while vertical lines represent locations where the seasonal range is estimated using the global relation presented in part (a) along with the known range in temperature from each locality (Table 1). The error associated with these estimates is on the order of several permil. In part (b), the seasonal range in the amount of precipitation is plotted against the seasonal range in $\delta^{18}O_{pt}$ values for all the weather stations in the IAEA/WMO network located in the tropics. Because of its island location, a relation fit only through the island data used to estimate the range in $\delta^{18}O_{pt}$ values for the site in the Philippines.

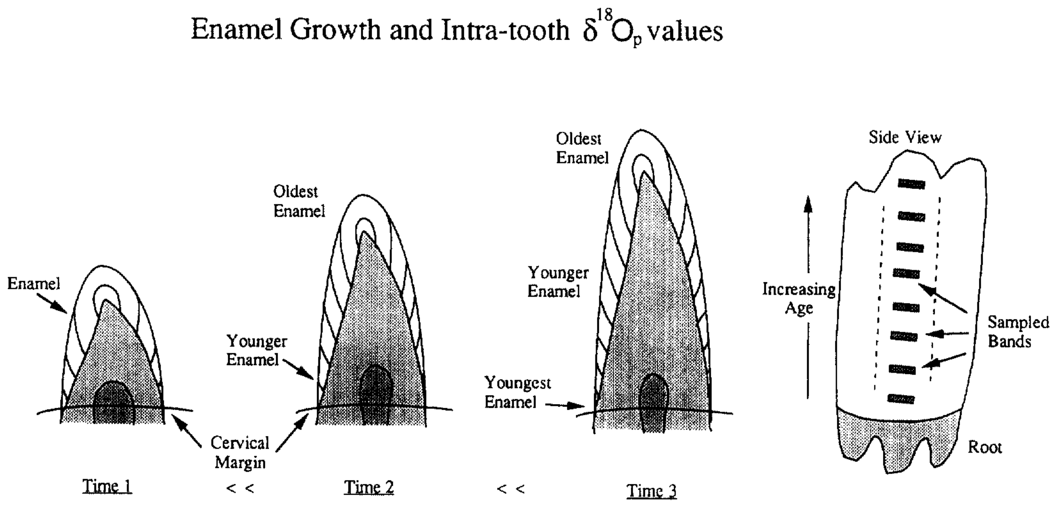

Fig. 2. Enamel growth and intra-tooth $\delta^{18}O_p$ values. Newly mineralized enamel formed below the cervial margin erupts out of the jaw, as is represented in cross section (Time 1). The first enamel to form is followed progesssively by younger and younger bands of enamel that form parallel to the cervical margin as eruption continues (Time 2 and 3). The result is a time-series of first-formed to last-formed enamel that can then be sampled from the surface of the tooth (last frame) to produce a time-series of $\delta^{18}O_p$ values. Time-series such as these are presented in Fig. 3.

Table 2. $\delta^{18}O_p$ (‰) versus relative height for all the sampled teeth. The height is the distance from the cervical margin in millimeters, and represents the time it takes for enamel to grow sequentially from the crown of the tooth to the cervical margin. In several cases seasonal cycles in $\delta^{18}O_p$ values were out of phase as the result of different seasons of birth for different individuals, and their positions were then modified in order to facilitate the comparison of intra-tooth ranges in $\delta^{18}O_p$ values between teeth. These modifications are noted next to the $\delta^{18}O_p$ values.

Sample	Height (mm)	δ18O Phosphate	Tooth/Offset	Sample	Height (mm)	δ18O Phosphate	Tooth/Offset
CATTLE - YORK				SHEEP - YORK			
YF8030-1-4	32.5	16.8	m3	YF8-S3-5	32	18.6	m3
YF8030-1-3	27.5	16.8		YF8-S3-4	27.5		
YF8030-1-2	21.5	17.1		YF8-S3-3	22.5	15.8	
YF8030-1-1	15	17.6		YF8-S3-2	17		
				YF8-S3-1	12	17.8	
YF8030-2-4	20	17.1	m3				
YF8030-2-3	13	17.7		YF8-Sa-6	28.5	17	m3
YF8030-2-2	8	17.2		YF8-Sa-5	23	15.7	
YF8030-2-1	2.5	16.3		YF8-Sa-4	17.5	16.3	
				YF8-Sa-3	13	18	
YF5591-1-6	37	16.5	m3	YF8-Sa-2	7	19	
YF5591-1-5	30	16.6		YF8-Sa-1	1	16	
YF5591-1-4	23	17.1					
YF5591-1-3	17	18.2		GRN-S1-4	16.5	12.7	M2/M3?
YF5591-1-2	9	18.5		GRN-S1-3	11	12.2	
YF5591-1-1	3	17.4		GRN-S1-2	7	11.5	
				GRN-S1-1	2.5	11.2	
FY4879-1-5	25	15.9	m3				
FY4879-1-4	20	16.3		CATTLE - FLORIDA			
FY4879-1-3	13	18.1		FLC-1-6	31	20.6	m3
FY4879-1-2	8	17.2		FLC-1-5	25	19.7	
FY4879-1-1	2.5	17.1		FLC-1-4	19	20.3	
				FLC-1-3	13	19.7	
YCOP-1-7	33	16	m3	FLC-1-2	7.5	20.2	
YCOP-1-6	27.5	16.1		FLC-1-1	2	19.8	
YCOP-1-5	21	16.7					
YCOP-1-4	15.5	17.7		FLC-2-11	39.5	19.5	m3
YCOP-1-3	9	17.2		FLC-2-10	35	19.9	
YCOP-1-2	2.5	16.4		FLC-2-9	32.5	20.5	
YCOP-1-1	1	16.1		FLC-2-8	30	21.3	
				FLC-2-7	24	22.5	
YCOP-2-5	27	15.9	m3	FLC-2-6	22	20.2	
YCOP-2-4	22	17.4		FLC-2-5	19	20.7	
YCOP-2-3	15.5			FLC-2-4	13.5	21.7	
YCOP-2-2	10	18.2		FLC-2-3	11.5	22	
YCOP-2-1	4	17.1		FLC-2-2	8.5	20.8	
				FLC-2-1	3	20.9	
YT3373-1-5	24	17	m3				
YT3373-1-4	18.5	17.5		FLC-3-4	13	19.5	m3
YT3373-1-3	13	17.8		FLC-3-3	9	19.7	
YT3373-1-2	8	17		FLC-3-2	5.5	20.4	
YT3373-1-1	3	16.5		FLC-3-1	2.5	19.5	
				CATTLE - IOWA			
SHEEP - YORK				IOW-1-6	26	15.6	m3
YF3354-S2-5	27.5	19	m3	IOW-1-5	22	15.6	
YF3354-S2-4	21	17.3		IOW-1-4	16	15.6	
YF3354-S2-3	15	15.2		IOW-1-3	13	15.6	
YF3354-S2-2	8	16.8		IOW-1-2	8	16	
YF3354-S2-1	2	19.3		IOW-1-1	3	16.8	
YCOP-S1-5	27	17.4	m3/-10	IOW-2-6	25	15.9	m3
YCOP-S1-4	21	16.4	-10	IOW-2-5	20.5	15.8	
YCOP-S1-3	14	15.6	-10	IOW-2-4	16	15.9	
YCOP-S1-2	8.5	16.7	-10	IOW-2-3	11	16.5	
YCOP-S1-1	2	18	-10	IOW-2-2	5.5	16	
				IOW-2-1	1	16.2	
YCOP-S2-6	34	17.8	m3/-9				
YCOP-S2-5	27		-9	IOW-3-5	30	16.1	m2
YCOP-S2-4	20.5	17.2	-9	IOW-3-4	23.5	16.2	
YCOP-S2-3	14	16.1	-9	IOW-3-3	17.5	16.2	
YCOP-S2-2	8.5	17.4	-9	IOW-3-2	12	16.6	
YCOP-S2-1	2	17.7	-9	IOW-3-1	7	15.7	

Table 2. (Continued)

Sample	Height (mm)	δ18O Phosphate	Tooth/Offset	Sample	Height (mm)	δ18O Phosphate	Tooth/Offset
ELK - CROATIA				ELK, CATTLE - WYOMING			
CR1-5	18.5	16.8	m3	WY-E1-5	51	11.6	m3/30
CR1-4	14.5	16		WY-E1-4	40	10.8	25
CR1-3	10			WY-E1-4	31	9.8	20
CR1-2	5.5	15.4		WY-E1-2	20	11.1	15
CR1-1	1	14.7		WY-E1-1	11	13.9	10
CR8-4	8.5	15.3	m3/-11	WY-E2-8	47.5	11.6	M3
CR8-3	3.5	15	-11	WY-E2-7	41	11.2	
CR8-2	-0.5	14.1	-11	WY-E2-6	35	9.83	
CR8-1	-6	15.1	-11	WY-E2-5	28	10.6	
				WY-E2-4	21	11.5	
CR11-5	16.5	16.2	m3	WY-E2-3	16		
CR11-4	13	16.3		WY-E2-2	9.5	13.1	
CR11-3	9.5	15.4		WY-E2-1	3	11.9	
CR11-2	5	15.1					
CR11-1	1	15		WY-E3-7	48	12.1	M3
				WY-E3-6	43	11	10
CR37-5	8	15	m3/-10	WY-E3-5	35.5	10.3	10
CR37-4	4	15.2	-10	WY-E3-4	30	10.5	10
CR37-3	-1	14.5	-10	WY-E3-3	23.5	11	10
CR37-2	-5.5	14.3	-10	WY-E3-2	18	12.9	10
CR37-1	-8.5	15.1	-10	WY-E3-1	13	13.7	10
CR39-5	22.5	16.6	m3/5	WY-C1-7	63	11.4	m3
CR39-4	19	16.8	5	WY-C1-6	56		
CR39-3	15	16.8	5	WY-C1-5	48	13.9	
CR39-2	11	15.7	5	WY-C1-4	41	9.8	
CR39-1	6	14.6	5	WY-C1-3	34	9.2	
				WY-C1-2	28	10.1	
SHEEP - ICELAND				WY-C1-1	21	11.2	
ICE-S12-6	33	16.3	m3				
ICE-S12-5	27.5	15.8					
ICE-S12-4	24	15.2		PIG - PHILIPPINES			
ICE-S12-3	19	14.7		PH88-6	40	16.9	c1
ICE-S12-2	13	16		PH88-5	32	16.6	
ICE-S12-1	7	16.5		PH88-4	25	16.7	
				PH88-3	17	17.3	
ICE-S4-5	19	14.5	m3/-4	PH88-2	8.5	17.7	
ICE-S4-4	14		-4	PH88-1	1	17.6	
ICE-S4-3	8.5	16.3	-4				
ICE-S4-2	2.5	16.9	-4	PH73-7	43.5	15.4	c1
ICE-S4-1	-3.5	15.1	-4	PH73-6	36.5	16	
				PH73-5	29	17.3	
ICE-S10-5	23		m3	PH73-4	21	16.5	
ICE-S10-4	18	14.3		PH73-3	12.5		
ICE-S10-3	13	15.9		PH73-2	7.5	16.2	
ICE-S10-2	7.5			PH73-1	1	15.6	
ICE-S10-1	2	16.9					
				PH89-6	38	16.4	c1
				PH89-5	29	17.1	
				PH89-4	20	16.9	
				PH89-3	13	16.5	
				PH89-2	7	16.8	
				PH89-1	1	16.2	

the cervical margin. This phenomenon is likely a result of differences in seasons of birth for different individuals and of the consequent differences in the onset of mineralization. When such offsets between teeth occurred, the relative sample positions were modified to bring all teeth from one locality into phase, and these modifications are noted in Table 2.

Average ranges in $\delta^{18}O_p$ values for each population of animals were determined by using $\delta^{18}O_p$ values that are $\pm 2\sigma$ from the mean as high and low endmembers (Table 3). Except for the teeth from Iowa and Florida, intra-tooth variations in $\delta^{18}O_p$ values for each population are relatively sinusoidal. The slightly larger amount of intra-populational error/scatter associated with the archaeological samples from York may be due to the greater range in time they represent (1000–400 yr B.P.).

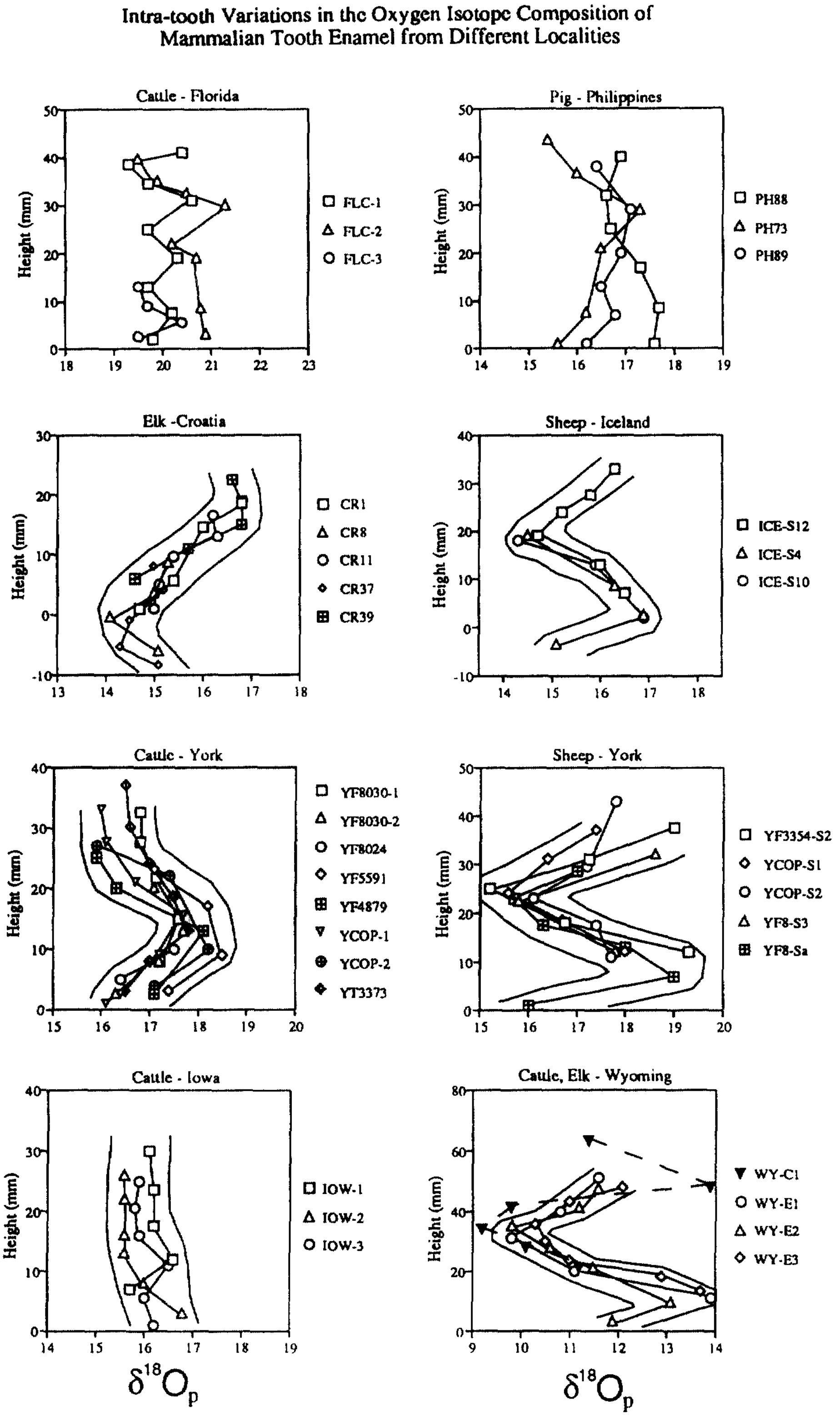

Fig. 3. Intra-tooth variations in $\delta^{18}O_p$ (‰) of mammalian tooth enamel for teeth from different localities. The data are plotted against relative position (Table 2), which represents time. Regular 'sinusoidal' variations in $\delta^{18}O_p$ values represent seasonal changes in $\delta^{18}O$ values of ingested water, and in general the amount of variation increases down each column in concert with differences in the range of local climate variables. The data for Iowa cattle are a noticible exception to this trend, as a larger intra-tooth range in $\delta^{18}O_p$ would be expected given the climatic similarity of Iowa and Wyoming. These animals, however, ingested ground water whose isotopic compostion does not vary seasonally. Also note the different intra-tooth range in $\delta^{18}O_p$ for cattle and sheep from York, which demonstrates the influence of diet on $\delta^{18}O_p$ values.

Table 3. Average intra-tooth ranges in $\delta^{18}O_p$ (‰) for each locality. Ranges are determined by using $\delta^{18}O_p$ values that are two standard deviations above and below the average value as represented by average summer and winter $\delta^{18}O_p$ values, respectively.

Samples	$\delta^{18}O_p$ Summer	$\delta^{18}O_p$ Winter	$\delta^{18}O_p$ Yearly Range	$\delta^{18}O_{pt}$ Yearly Range
Cattle, WY	13.9	9.7	4.2	7.6
Elk, WY	13.8	9.8	4.0	"
Elk, Croatia	16.8	14.3	2.5	5.7
Sheep, Iceland	16.9	14.3	2.6	3.0
Sheep, York	19.0	15.6	3.4	3.1
Cattle, York	18.2	15.9	2.3	"
Pig, Phil.	17.7	15.9	1.8	3.3

5. DISCUSSION

5.1. Ingested Water and Intra-Tooth Variations in $\delta^{18}O_p$ Values

Although it has usually been assumed that intra-tooth variations in $\delta^{18}O_p$ values of mammalian tooth enamel are due only to seasonal variations in the isotopic composition of ingested water, there has never been independent evidence that rules out the possibility that some other factor like seasonal changes in metabolic processes occurring within an animal itself may be the source of some or all of the intra-tooth variations. The oxygen isotope data for the Iowa and Wyoming samples, however, indicate that, at least under the conditions of this study, the variations are directly related to variations in $\delta^{18}O$ of ingested water and not to temporal variations in the kind and intensity of physiological processes utilized by a given mammal.

The Wyoming cow and other animals were free ranging, and, therefore, they ingested water from surface reservoirs that should mirror local precipitation. In keeping with the wide seasonal range in temperature and $\delta^{18}O_{pt}$ values in this area (Table 1), the intra-tooth variations in $\delta^{18}Op$ values are large (4‰). The mean annual range in temperature (MART) in Iowa is roughly similar to that of Wyoming (Table 1), and thus it would be reasonable to expect that the intra-tooth variations in $\delta^{18}O_p$ values would be similar if individuals from both localities were drinking the same types of surface waters during the period of enamel formation. The cows from Iowa, however, were given dry food to eat, and thus relied primarily on tap water from the city of Ames to satisfy their water needs. This tap water comes from groundwater whose $\delta^{18}O$ value is constant over the time that the animals lived and which should be equal to the weighted mean value for local precipitation over a number of years (e.g., Fritz et al., 1987). This lack of isotopic variation in ingested water is reflected in the lack of isotopic variation in the teeth of the Iowa cows (Fig. 3) and demonstrates the dominance of ingested water in determining $\delta^{18}O_p$ values. More importantly, these data demonstrate that in the absence of isotopically variable water, there is an insignificant amount of variation in $\delta^{18}O_p$ associated with seasonal changes in the metabolism of bovids that are not experiencing extreme dietary stress or environmental conditions.

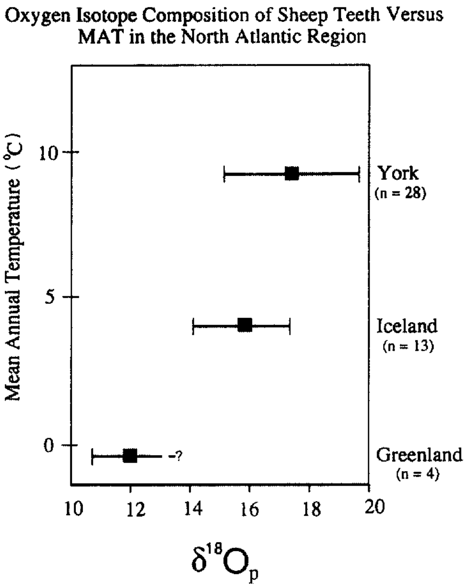

Fig. 4. Average $\delta^{18}O_p$ (‰) of sheep teeth $\pm 2\sigma$ vs. mean annual temperature in the north Atlantic region. $\delta^{18}O_p$ values for the samples from each locality vary regularly with the mean annual temperature, indicating that information on both average climate and seasonal variations is reflected by phosphate oxygen. Only four samples from a single tooth could be sampled from Greenland, and they do not represent a complete year. Therefore, the average $\delta^{18}O_p$ in this case may be slightly inaccurate.

5.2. Comparison between $\delta^{18}O_p$, $\delta^{18}O_{pt}$, and Climate Variables

Because intra-tooth variations in $\delta^{18}O_p$ values are influenced primarily by changes in the isotopic composition of ingested water, there should be observable differences in the range of these values associated with climate variables that control the isotopic composition of precipitation at each of the sampled localities. Such differences are in fact quite apparent, particularly for samples from higher-latitude sites where temperature is strongly correlated with $\delta^{18}O_{pt}$ values. In the case of the north Atlantic region, the different seasonal range in temperatures in Iceland and England are reflected by different seasonal ranges in $\delta^{18}O_{pt}$ of 2.0 and 3.1‰, respectively (Table 1). In turn, the intra-tooth range in $\delta^{18}O_p$ values is 2.6‰ for sheep from Iceland and 3.4‰ for sheep from England. Thus the seasonal differences in both temperature and $\delta^{18}O_{pt}$ values are recorded by phosphate oxygen. The connection between temperature, $\delta^{18}O_{pt}$, and $\delta^{18}O_p$ is reinforced by the observed progression from lower $\delta^{18}O_p$ values in Greenland to higher $\delta^{18}O_p$ values in York that is associated with changes in mean annual temperature (Fig. 4).

The $\delta^{18}O_p$ data for elk from Croatia and Wyoming also capture regional trends in average and seasonal variations in $\delta^{18}O_{pt}$ values. For example, the winter and mean annual temperatures in Wyoming are the lowest of any sampled site, and accordingly the elk from Wyoming have the lowest $\delta^{18}O_p$ values. In addition, the difference in the seasonal range in temperature between Wyoming (26°C) and Croatia (19°C) is mirrored by the seasonal ranges of $\delta^{18}O_{pt}$ values of ~7.5‰ in Wyoming and of 5.7‰ in Croatia and is recorded by the intra-tooth variations in $\delta^{18}O_p$ values of 4‰ and 2.5‰, respectively. It is clear, however, that the intra-tooth variations in $\delta^{18}O_p$ values are much smaller than the seasonal variations in $\delta^{18}O_{pt}$ values, and they are not as great as might be expected in light of the data for sheep from the north Atlantic.

At low latitudes, the *amount* of precipitation that falls from an airmass rather than temperature is more strongly correlated with the oxygen isotope composition of precipitation (Fig. 1b). Although we have samples from only one tropical locality, the data are consistent with seasonal variations in the amount of rainfall determining the range of intra-tooth variations in $\delta^{18}O_p$ values of the pig teeth. While the seasonal range in temperature in the Philippines varies only one or two degrees Celsius over the course of the year, the amount of precipitation is highly variable as a result of monsoonal conditions prevailing in that region, with ~230 mm more rain falling in the summer than in the winter (Table 1). This difference results in an estimated seasonal range in $\delta^{18}O_{pt}$ values of 3.2‰ (Fig. 1b) which is expressed in the regular 1.8‰ variations in $\delta^{18}O_p$ values of the pig teeth.

Differences in the annual amount of precipitation can also account for the similarity in average $\delta^{18}O_p$ values for animals living in the Philippines and those living in the north Atlantic region. The annual amount of precipitation in the York region is only 600 mm, while at the northern part of Luzon Island it is nearly three times as great at 1765 mm/yr (Table 1). The result of concentrated rainout from the air masses which pass over the Philippines is the progressive removal of ^{18}O from the air mass, and thus lower $\delta^{18}O_{pt}$ values of the remaining water vapor (e.g., Dansgaard, 1964). Therefore, the similarity in $\delta^{18}O_p$ values between samples from York and the Philippines has a basis in the higher proportion of air mass rainout in the tropics relative to the mid- to high-latitudes and is largely coincidental.

In contrast to the localities described above, there are areas of the world where the differences between summer and winter $\delta^{18}O_{pt}$ values are minimal (data points with values close to zero on the vertical axis of Fig.1). These areas represent transitional zones where neither the amount of rainfall nor temperature is strongly correlated with $\delta^{18}O_{pt}$ values, and where intra-tooth variations in $\delta^{18}O_p$ values would also be expected to be minimal. The samples from Florida fall into this transitional zone (Table 1; Fig. 1) which may explain why they exhibit the smallest range in intra-tooth $\delta^{18}O_p$ values of any of the materials analyzed in this study.

5.3. Influence of Factors Other Than $\delta^{18}O_{pt}$ on $\delta^{18}O_p$

The data presented above provide strong evidence that intra-tooth ranges in $\delta^{18}O_p$ mirror similar changes in seasonal ranges of the $\delta^{18}O$ value of precipitation, which is in turn related to continental climate variables such as temperature at mid- to high-latitudes, and the amount of precipitation at lower latitudes (Table 3). Not unexpectedly, ranges in $\delta^{18}O_p$ values are smaller than corresponding ranges in $\delta^{18}O_{pt}$ values. A reasonable explanation for this effect is the contribution of atmospheric oxygen which has a constant $\delta^{18}O$ value, which thus dampens variations in the $\delta^{18}O$ value of body water relative to that of ingested water by ~25%. In addition, the data indicate that animal behavior affects intra-tooth ranges in $\delta^{18}O_p$ values by determining how much ingested water comes from different sources, and that local hydrological conditions may play a role in determining intra-tooth ranges in $\delta^{18}O_p$ values in some cases.

5.3.1. Large intra-tooth ranges in $\delta^{18}O_p$ for sheep

Intra-tooth ranges in $\delta^{18}O_p$ for sheep from Iceland and York (2.6 and 3.4‰, respectively) are very close to seasonal variations in $\delta^{18}O_{pt}$ (3.0 and 3.1‰, respectively) despite the role that atmospheric oxygen should have in dampening the precipitation signal. These large ranges probably reflect the dietary behavior of sheep, in particular the ingestion of a large proportion of leaf water during the summer months. Summer diet is important because leaf water from actively growing plants is more available to sheep during this time. In addition, leaf water has higher $\delta^{18}O$ values than local precipitation due to evaporation at the leaf surface (e.g., Flanagan et al., 1991), an effect that is greater when ambient relative humidity is lower (e.g., Craig and Gordon, 1965) as it is in summer relative to winter (Table 1).

5.3.2. Different intra-tooth ranges in $\delta^{18}O_p$ for York cattle and sheep

It is likely that leaf water also plays a role in causing the different ranges in intra-tooth $\delta^{18}O_p$ values that are observed for sheep and cattle from York (3.4 and 2.6‰, respectively). The effect of leaf water on $\delta^{18}O_p$ values should be different for sheep and cattle because they have different dietary habits and, therefore, ingest different proportions of leaf water at any given time. Sheep have been described as selective grazers, and they are most likely to eat more leaves of grass relative to total organic material and less dead (dry) material relative to live (water-filled) material (Hulet et al., 1975). Cattle are also grazers and eat grass leaves, but they are less selective and are thus more likely to eat a higher percentage of dead (dry) plant material and, therefore, drink more surface water relative to sheep (Hafez, 1975). Therefore, the body water of sheep, and hence their $\delta^{18}O_p$ values, will be more affected by ^{18}O-enriched leaf water. A comparison of data from sheep and cattle support the hypothesis that the effect of leaf water is greatest during summer months. Low winter $\delta^{18}O_p$ values for both sheep and cattle are similar, while the higher summer $\delta^{18}O_p$ values of sheep are ~0.8‰ higher than corresponding summer values for cattle (Fig. 3). This observation is consistent with the lower relative humidities and abundance of leaves that characterize summer months.

5.3.3. Small intra-tooth ranges in $\delta^{18}O_p$ for Wyoming and Croatia mammals

In the case of the Wyoming and Croatian elk, the intra-tooth variations in $\delta^{18}O_p$ values are smaller than expected. Assuming atmospheric oxygen accounts for ~25% of the oxygen flux, first order estimates of intra-tooth ranges in $\delta^{18}O_p$ for elk from Wyoming and Croatia would be 5.7 and 4.3‰, respectively, while the observed ranges are 4.0 and 2.5‰, respectively. On the basis of data for sheep and cattle from the North Atlantic, there is no reason to believe that small ranges in $\delta^{18}O_p$ are due to the ingestion of leaf water.

It is possible, however, that small ranges in $\delta^{18}O_p$ values are due not to mammal behavior, but to external hydrological factors that reduce the ability of surface water reservoirs to track seasonal changes in the $\delta^{18}O$ of precipitation in certain areas. For example, precipitation falling as snow in Wyoming does not immediately enter surface water reserviors such as streams, ponds, or plants. Therefore, it is possible that much of this precipitation may be lost as spring snowmelt before it can be ingested to any significant degree by local mammals. Similarly, in seasonally arid regions such as Wyoming and Croatia, it is possible that the volume of precipitation representing one the seasonal extremes in $\delta^{18}O_{pt}$ values is not large enough to alter the $\delta^{18}O$ value of elk body water appreciably. Such underrepresentations of seasonal extremes in $\delta^{18}O_{pt}$ values may explain why intra-tooth ranges in $\delta^{18}O_p$ values are smaller than expected and may be common in seasonally snow covered or arid regions.

Lastly, it should be noted that although seasonal changes in physiological processes did not affect the range in intra-tooth $\delta^{18}O_p$ values significantly in the Iowa cattle, it is possible that changing physiological processes could have affected the intra-tooth range for elk living in Croatia and Wyoming. As free ranging animals, the elk may have undergone dietary stress during winter months that may have modified their normal metabolic patterns. In addition these elk experienced more arid conditions during the summer months than the other animals, and this may have modified the amount of water lost through the skin as sweat or transcutaneous water vapor as well as the isotopic fractionations associated with these processes (Kohn, 1996).

5.3.4. Seasonal changes in the influence of different factors

From the intra-tooth data of sheep and cattle it appears that the influence of water ingested from plant leaves on $\delta^{18}O_p$ is not the same throughout the year. This is due either to a decrease in the proportion of leaf water ingested by sheep in winter, an increase in relative humidity during winter, or a combination of both effects. In addition, it is possible that small intra-tooth ranges in $\delta^{18}O_p$ of the Wyoming and Croatia samples are a result of hydrological and physiological processes that are not necessarily constant throughout an entire year. Therefore, it is clear that seasonal variability in the relative importance of different behavioral, physiological, and hydrological factors *itself* is an additional factor that plays a role in determining how $\delta^{18}O_p$ values are related to $\delta^{18}O_{pt}$ values, and that this factor is unique to the study of intra-tooth variations.

5.4. Quantifying Relations between $\delta^{18}O_p$ and $\delta^{18}O_{pt}$

Given the number of different factors that may be introduced *via* physiology, behavior, and perhaps even local hydrology, it is a challenge to relate accurately a range in $\delta^{18}O_p$ values to a range in $\delta^{18}O_{pt}$ values with the goal of estimating seasonality. One possible method of doing this involves the use of physiological models that combine estimates of fluxes of O_2, H_2O, and CO_2 into and out of the body of a mammal, and the isotopic fractionation associated with these processes, to calculate the relation between $\delta^{18}O_p$ and $\delta^{18}O_{pt}$ (e.g., Luz et al., 1984; Ayliffe and Chivas, 1990; Bryant and Froelich, 1995; Kohn, 1996). The effects of dietary preferences, in particular ingested leaf water, can be incorporated into these models by considering relative humidity as an independent variable (e.g., Ayliffe and Chivas, 1990; Kohn, 1996). Thus physiological models may be able to account for many aspects of mammalian physiology and dietary behavior. They cannot, however, be easily modified to account for external hydrological factors, or seasonal variations in the relative importance of different factors.

As an alternative to physiological models it is possible to use empirical relations between $\delta^{18}O_p$, $\delta^{18}O_{pt}$, and relative humidity that are constructed by comparing isotopic and climatic data from different geographic localities (e.g., Luz et al., 1990). In contrast to physiological modeling, empirical relations do not involve making estimates of oxygen fluxes and fractionation factors associated with mammalian physiology. Instead they are a 'black box' approach in which it is assumed that differences in $\delta^{18}O_p$ can be reflected almost completely by differences in the $\delta^{18}O$ value of local precipitation and relative humidity, and that the influence of other aspects of behavior, physiology, and hydrology on $\delta^{18}O_p$ - $\delta^{18}O_{pt}$ relations remains constant.

Given the lack of precise knowledge regarding the $\delta^{18}O$ of water ingested by the animals in this study, it is not possible to use our data to test precisely how well the physiological models relate $\delta^{18}O_p$ to $\delta^{18}O_{pt}$, or whether factors other than relative humidity-leaf water have a significant impact on this relation. Similarly, there is not enough data to construct new empirical relations between $\delta^{18}O_p$, $\delta^{18}O_{pt}$, and relative humidity. The data do, however, provide a basis for making suggestions as to the type of future work that needs to be conducted. Most importantly, analyses need to be made of teeth from animals for whom there is a reasonable knowledge of the different sources of water they ingested, the fluxes and isotopic composition of water into and out of their bodies, and how these variables change over the course of a year. Included in these studies should be animal populations living in a wide variety of environments so the effects of hydrological factors and environmental extremes in cold or aridity on the $\delta^{18}O_p$ - $\delta^{18}O_{pt}$ relation can be investigated. Lastly, it is necessary that oxygen isotope data be collected for species with different dietary habits, in particular species that rely on significantly different proportion of ingested leaf water. Only by comparing data from such pairs of species is it possible to evaluate independently the effect of relative humidity on the relation between $\delta^{18}O_p$ and $\delta^{18}O_{pt}$, as has been noted by previous authors (Luz et al., 1990; Kohn, 1996). Carnivore-herbivore pairs may be particularly well suited for such a comparison, although herbivore pairs such as sheep and cattle may work as long as their intra-tooth ranges in $\delta^{18}O_p$ values are consistently different.

5.5. Other Applications of Intra-Tooth Variations in $\delta^{18}O_p$

Although not the main focus of this paper, the widespread occurrence of intra-tooth variations in $\delta^{18}O_p$ values demonstrated here has appreciable significance for studies of long-term climate change and paleobiology. In the case of the former, seasonal variations in $\delta^{18}O_p$ of several permil that can occur within single teeth are likely to be on the same order of magnitude as changes in *average* $\delta^{18}O_p$ values of teeth of different ages (see Fricke *et al.*, in review). If intra-tooth variations in $\delta^{18}O_p$ are not accounted for, then oxygen isotope data for a single time period could be biased away from average $\delta^{18}O_p$ values and towards seasonal extremes. The result of biased data is a decreased ability to resolve long-term climate change. Several past studies of climate change using $\delta^{18}O_p$ values relied on the analysis of all the enamel on a tooth (e.g., Bryant et al., 1994; Huertas et al., 1997) and, depending on tooth wear, these bulk $\delta^{18}O_p$ may not be providing completely accurate paleoclimate information.

Intra-tooth variations in $\delta^{18}O_p$ can be used to study paleobiology because high summer values and low winter values act as temporal markers. These markers can be used to study the rates of a variety of biological processes including rates of enamel mineralization and dental development, which are in turn dependent on rates of overall physiological development. In addition they have the potential to provide information on the season in which a particular individual was born, and in the case of juveniles, the season in which it died. Therefore, studies of intra-tooth variations in $\delta^{18}O_p$ may be of great value in learning more about anthropology, paleobiology, and evolution.

6. SUMMARY AND CONCLUSIONS

The data from this study represent an important stage in the development of a proxy for seasonal variations in continental climate variables that is based on intra-tooth variations in the $\delta^{18}O$ value of mammalian tooth enamel phosphate. Oxygen isotope data for teeth of mammal herbivores that lived over a wide range of climatic conditions demonstrate that intra-tooth $\delta^{18}O_p$ values mirror both seasonal and mean annual differences in the $\delta^{18}O$ value of local precipitation, which are in turn associated with changes in climate variables such as temperature (at higher latitudes) and the amount of precipitation (in the tropics). Therefore, we can be confident that intra-tooth variations in $\delta^{18}O_p$ at least provide accurate qualitative estimates of seasonality in continental environments. This is an important advance because even qualitative proxies for seasonality are uncommon at this time. In addition, this study demonstrates that qualitative paleoclimatic information can be obtained from intra-tooth $\delta^{18}O_p$ values even when knowledge of physiology, behavior, and local hydrological conditions is limited, which may be the case when dealing with ancient or extinct populations of mammals.

The greastest challenge that lies ahead is the quantitative interpretation of a range of $\delta^{18}O_p$ values in terms of a corresponding range in the $\delta^{18}O$ values of local precipitation. Of the several physiological, behavioral, and possibly hydrological factors that complicate this relation, the ingestion of leaf water having $\delta^{18}O$ values higher than local precipitation probably plays the biggest role in modifying intra-tooth ranges in $\delta^{18}O_p$ of mammal herbivores. Both physiological models and empirical relations have the potential to provide more quantitative relations between $\delta^{18}O_p$ and $\delta^{18}O_p$, but more studies of teeth from well-constrained populations of mammals living under a variety of environmental conditions are needed.

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