ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 126 (1996) 91–99

PALAEO

Inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: implications for palaeoclimatological and palaeobiological research

Henry C. Fricke, James R. O'Neil

Department of Geological Sciences, University of Michigan, Ann Arbor, MI 48104-1063, USA

Received 23 June 1995; revision 5 October 1995; accepted 2 May 1996

Abstract

Significant differences in the $\delta^{18}O_p$ value between teeth, and even within a single tooth were observed in a detailed study of the oxygen isotope composition of tooth enamel phosphate ($\delta^{18}O_p$) of hypsodont teeth from bison and sheep jaws. The permanent molars and premolars of a fossil adult bison from eastern Wyoming (~500 yr B.P.) and a modern sheep from California were analyzed. The bison is assumed to have been free-ranging with a variety of possible water sources, whereas the sheep was raised on a ranch. Inter-tooth variability in $\delta^{18}O_p$ for the bison compared to the sheep (5.6‰ and 3.5‰, respectively) may be a result of behavioral differences. Analyses of multiple samples from the m3 of both the bison and sheep vary to a similar degree (3.5‰) in a similar cyclic pattern down the length of the tooth, a pattern which is interpreted to be seasonal. When present, inter- and intra-tooth variations in $\delta^{18}O_p$ are controlled by the water and food ingested by the mammals during the period of enamel formation. In these localities, well waters, surface waters, and mother's milk have different isotopic compositions at different times of the year.

The data underscore the role of biology and behavior in determining $\delta^{18}O_p$ values, and the need to understand how they vary for a population of interest. If these variations are taken into account, the $\delta^{18}O_p$ values of single samples from small, late-forming teeth (e.g. premolars) can be used as a proxy for the $\delta^{18}O$ value of local meteoric water for long-term climate studies. Multiple samples from a single third molar may provide information on the duration and timing of enamel growth, seasonality, as well as long-term climate change.

1. Introduction

Because tooth enamel has a lower organic content, is denser, and comprises larger apatite crystals relative to dentine and bone, it is more resistant to physical and chemical alteration and has become the material of choice in paleoclimatic research using oxygen isotope analyses of biogenic phosphate (e.g. Ayliffe et al., 1994; Bryant et al., 1994; Fricke et al., 1995). Early researchers in this field realized that the constant body temperature of mammals made it possible to interpret the oxygen isotope composition of tooth enamel phosphate ($\delta^{18}O_p$) as a reflection of the isotopic composition of local precipitation ($\delta^{18}O_w$) that they were drinking (e.g. Longinelli, 1984; Luz et al., 1984), which in turn is a proxy for local average surface temperature (Dansgaard, 1964; Rozanski et al., 1993). Thus mammalian remains collected from different geological or archaeological strata

0031-0182/96/$15.00 © 1996 Elsevier Science B.V. All rights reserved
PII S0031-0182(96)00072-7

at a single locality can be used to reconstruct climate and rate of climate change over relatively long periods of time (e.g. Fricke et al., 1995).

An inherent assumption of this method is that change in $\delta^{18}O_p$ of samples separated by years, decades, or more, is due only to changes in climatic variables such as temperature, relative humidity, air mass source, etc. over that period. This relation for hypsodont (high crowned) teeth that form over a period of months can be complicated by short-term seasonal changes in $\delta^{18}O_w$ that occur during enamel formation. For a single individual these changes can result in large inter- and intra-tooth variations in $\delta^{18}O_p$ not related to long-term climate. Therefore variations in $\delta^{18}O_p$ values of different teeth from a given geological or archaeological deposit could be influenced by a tooth sampling bias, and change in $\delta^{18}O_p$ over time may not have any relation to long-term climate change. To minimize this effect in their study of $\delta^{18}O_p$ variations in Pleistocene bear teeth, Reinhard et al. (1996–this issue) analyzed tooth enamel from canine teeth only.

The object of this study is to describe possible seasonal effects of the oxygen isotope composition of both drinking water ($\delta^{18}O_d$) and plant water ($\delta^{18}O_{pw}$) on $\delta^{18}O_p$ of a domesticated sheep and a wild bison. It becomes apparent that the biology and behavior of the individuals sampled for paleoclimatological research can play an important role in determining enamel $\delta^{18}O_p$ values, as has been observed in the oxygen isotope composition of the CO_3 fraction of dentine from bears and extinct proboscideans (Koch et al., 1989). Therefore it is necessary to characterize how both biology and behavior will effect $\delta^{18}O_p$ for a given population so that the change in $\delta^{18}O_p$ associated with long-term climate only can be isolated. With these effects in mind, paleoclimate sampling strategies include taking single samples from small, late-forming teeth that can be still be used as an record of long-term change, and multiple samples from a single tooth can be interpreted as a record of seasonal differences in $\delta^{18}O_w$, as well as long-term climate.

2. Sampling

The teeth analyzed include the permanent lower premolars (p2–p4) and molars (m1–m3) from a young adult (m3 just coming into wear) sheep that was raised this past decade on a ranch in northern California, and the same selection of teeth from a young adult bison living about 500 yr B.P. in eastern Wyoming. The numbers associated with each tooth type shown in Fig. 1 are related to the relative position of the tooth in the jaw. The sheep had a fairly well known life history, including a known diet, and a restricted range. As a domesticated animal its living conditions are considered fairly representative of sheep found in the archaeological record. In contrast, the bison was a wild animal killed by native Americans as part of a herd drive at the Vore buffalo jump site (Reher and Frison, 1980). Little is known for certain about the behavior of bison from this period (J. Speth, pers. comm.), but without human domestication it should have had much in common with the large wild mammal herbivores commonly found both today and in the geological record.

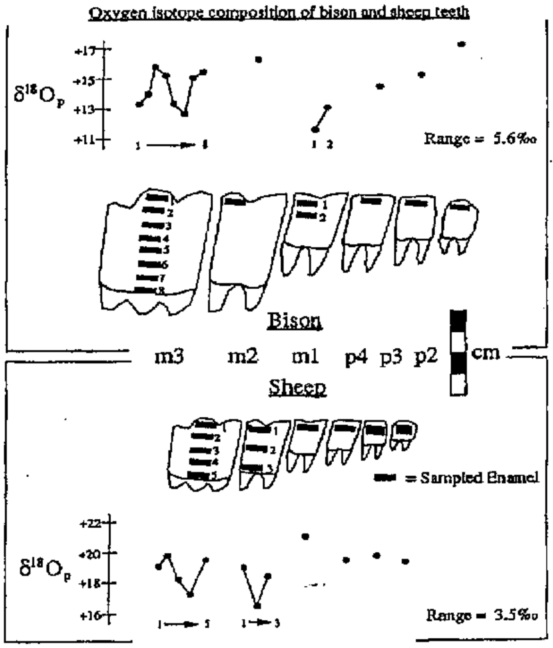

Fig. 1. Schematic diagram of teeth from the lower jaws of a fossil bison and a modern sheep, the enamel sample locations (center), and corresponding $\delta^{18}O_p$ values (above and below).

Samples of ~40 mg were ground from the enamel of each of the teeth as ~3 mm bands parallel to the occlusal surface (Fig. 1). Due to the incrementally layered growth structure of enamel, such bands should sample material that forms over roughly the same time period (Fig. 2). The m3 from both the sheep and bison were sampled at regular intervals up from the cervical margin, with a total of five samples coming from the sheep m3, and eight from the bison m3 (Fig. 1). The number of samples that it is possible to take is limited by the size of the tooth. For the sheep p2 and p3 it is difficult to sample more than one horizontal band with our present techniques (Fig. 1).

3. Analytical techniques and results

In the method of phosphate analysis utilized in our laboratory, the phosphate radical is isolated as Ag_3PO_4, which is then reacted with graphite in silica-glass tubes at 1400°C to form CO_2 which in turn can be directly introduced to the inlet system of a mass spectrometer (O'Neil et al., 1994). Using this technique we obtain a value of 21.8 ± 0.2‰ for NBS-120c, which is comparable to the values obtained using the conventional fluorination method. Results are shown in Table 1 for both the bison and sheep teeth.

The $\delta^{18}O_p$ values of seven of the twelve sheep samples fall between 19.0 and 19.8‰, including the samples from the three premolar teeth (Fig. 1; Table 1). The m1 sample has an anomalously high $\delta^{18}O_p$ value of 21.0‰. For both the m3 and m2, which were sampled more than once, some $\delta^{18}O_p$ values fall below those constituting the main group by as much as 3.5‰, and in both cases they define a cyclic pattern down the length of the tooth (Fig. 1). In contrast, the $\delta^{18}O_p$ values of bison samples, including the three different premolar

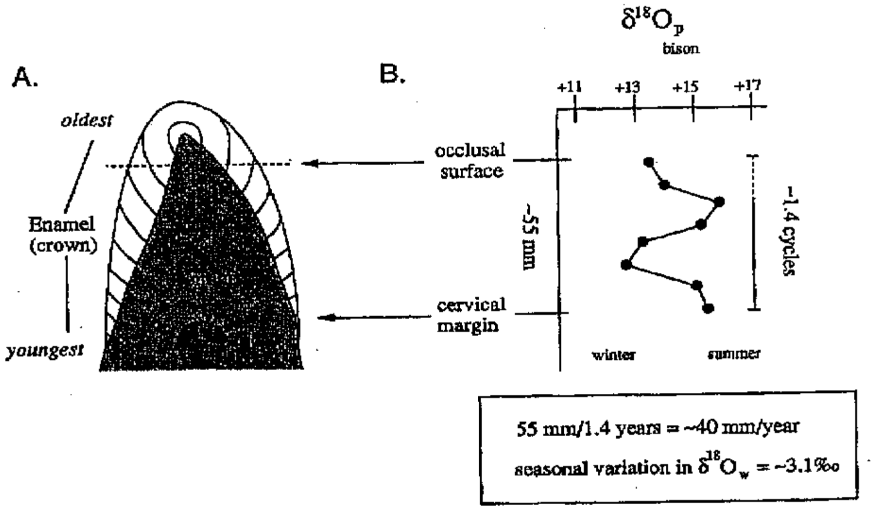

Fig. 2. A. Schematic cross section of an unworn tooth (after Hillson, 1986). Note incrementally layered growth structure of tooth enamel whose horizontal rings form over a short time span. Enamel formation begins at the crown and continues downward toward the cervical junction. Position of the occlusal surface, which forms as a tooth undergoes continued wear, is represented by the dotted line. B. $\delta^{18}O_p$ variation in the bison m3 versus sample position as represented in part (A). These data provide an example of how the $\delta^{18}O_p$ values can be used to estimate the growth rate and season of growth for a given tooth/species. About 1.4 cycles occur over the length of the tooth (~55 mm), a growth rate of about 40 mm/cycle. Each cycle is interpreted to represent a one-year growth in enamel, with the high $\delta^{18}O_p$ values indicative of summer growth, and the low $\delta^{18}O_p$ values of winter growth. An estimate of seasonality is the difference between the two, which is ~3.5‰. The tooth has experienced little wear, thus all the enamel formed on the order of 1.5 years.

Table 1
Oxygen isotope composition of tooth enamel from the sheep and bison jaws described in the text. The first set of characters indicates the tooth sampled, and the second set the location of the sample as shown in Fig. 1. Material from each sampled band was analyzed at least twice, with an average reproducibility of approximately 0.2‰

Tooth	Position	$\delta^{18}O_p$ (SMOW)
Bison		
p2		17.3
p3		15.2
p4		14.1
m1	1	11.7
	2	13.0
m2		16.3
m3	1	13.5
	2	14.0
	3	15.8
	4	15.2
	5	13.2
	6	12.7
	7	15.1
	8	15.4
Sheep		
p2		19.3
p3		19.7
p4		19.5
m1		21.0
m2	1	19.0
	2	16.5
	3	18.5
m3	1	19.0
	2	19.8
	3	18.2
	4	17.2
	5	19.5

samples, are quite variable (Fig. 1; Table 1). Also the $\delta^{18}O_p$ values of the m1 teeth are on average lower than all the other values. The eight analyses of the bison m3 have a range of 3.5‰, and define an even more obvious cyclic trend (Fig. 1).

4. Discussion

Many of the mammalian species which have been described as potentially useful for paleoclimatic research are relatively common herbivores such as sheep, horses, cattle, and deer (D'Angela and Longinelli, 1990; Luz et al., 1990; Bryant et al., 1994). The teeth of these mammals, and of bison, are high-crowned (hypsodont), and represent incrementally layered growth bands of enamel (Fig. 2). As mentioned above, the oxygen isotope composition of this tooth enamel depends primarily on the composition of the water the animal is ingesting during enamel formation. This growth occurs on the order of months so that both the timing and duration of enamel formation, and seasonal variations in drinking water and food sources, must be considered when evaluating its use as a climate proxy.

4.1. Formation of tooth enamel in permanent cheek teeth

The formation of the hydroxyapatite prisms which constitute mammalian tooth enamel takes place by a process known as mineralization or maturation (see Hillson, 1986 and Davis, 1987 for detailed reviews of mammalian dental development). For the lower cheek teeth of sheep and cattle, the duration over which mineralization takes place is depicted in Fig. 3. Because there has been no investigation of bison populations, the mineralization schedule for cattle, which is a close relative, is used as a proxy (Brown et al., 1960). For the sheep, the mineralization interval of each tooth is bounded by the age of eruption, and not by the time when crown formation was completed (Silver, 1969). Therefore the intervals for sheep may by overestimates.

Except for the first molar, tooth enamel for both animals forms roughly over a time interval of 0.5–2 years after birth (Brown et al., 1960; Silver, 1969; Hillson, 1986). It is important to emphasize that the length of the interval and the age when it begins are variable. Both are related to the physiological development of an individual, and can be affected by biological and environmental factors such as the sex, size, health, and diet of the individual (Hillson, 1986; Smith, 1991).

For $\delta^{18}O_p$ values, any variation in the isotopic composition of ingested water over the interval of formation will be "recorded" by the growing enamel. If the animal is ingesting water which undergoes seasonal changes in $\delta^{18}O_w$ values, it will be possible to refine estimates of the time interval

, and of
d repre-
: enamel
isotope
primar-
nimal is
growth
›oth the
on, and
ıd food
ating its

ıt cheek

prisms
el takes
ıtion or
1987 for
levelop-
eep and
ılization
here has
›ns, the
; a close
, 1960).
of each
and not
mpleted
›r sheep

for both
erval of
); Silver,
ıphasize
when it
physio-
l can be
factors
of the

isotopic
erval of
growing
: which
s, it will
interval

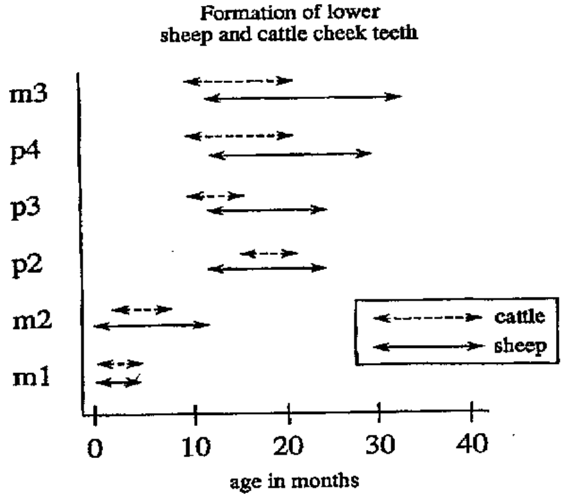

Fig. 3. Estimated age and interval over which enamel formation takes place for sheep and cattle (Silver, 1969; Brown et al., 1960). The relative timing is related to the eruption sequence of the teeth (m1–m3), but can vary depending on biological and environmental fartors. The $\delta^{18}O_p$ value of the tooth enamel will depend on the isotopic composition of water ingested during the interval of formation.

and the time of year over which enamel forms. For example, the cyclic nature of the $\delta^{18}O_p$ of bison m3, and to a lesser extent sheep m3, allow quantitative estimates to be made of rates of enamel growth. The $\delta^{18}O_p$ values of bison m3 cycle approximately 1.4 times, over a 55 mm length of enamel (Fig. 2). Assuming that the cyclicity is mirroring seasonal variations in the $\delta^{18}O$ value of ingested water, this cyclicity corresponds to an enamel growth rate of ~40 mm/yr (Fig. 2). Similarly, the sheep m3 has a calculated growth rate of ~25 mm/1.2 yr, or ~21 mm/yr. The high $\delta^{18}O_p$ values at the cervical margin of the bison m3 demonstrate that the last enamel to form did so in the summer, while the low values of the oldest enamel imply that mineralization began in the winter or early spring (Fig. 2). Similar investigations could be done for all the teeth, the compilation of such data providing information on the season of birth and overall dental development by delineating the length of time and season(s) of enamel formation for each tooth of these individuals. Finally, despite the inferred seasonality in this case, it should be emphasized that there are many situations possible in nature where ingested water *will not* have seasonal variations associated with the $\delta^{18}O$ value of ingested water.

4.2. The m1 and water sources prior to weaning

Because m1 teeth of sheep and cattle are known to form prior to birth (Brown et al., 1960; Weinreb and Sharav, 1964; Hillson, 1986), the m1 enamel of some of the sheep, and probably the bison, must have formed in vitro from the body water of the mother. Similarly, milk from the mother ingested following birth and prior to weaning, also forms from the mother's body water. This body water has already undergone fractionation to values higher than those of local meteoric water (D'Angela and Longinelli, 1990) as a result of metabolic processes (e.g. Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995). As a result, the $\delta^{18}O_p$ of the m1 is unlikely to reflect the value of local meteoric water, as has been modeled recently for a mother/foal horse pair by Bryant et al. (1996a).

The season of birth of the individual will play the key role in determining how the different pre-weaning water sources will affect the $\delta^{18}O_p$ values of the m1 relative to those of the later forming teeth. In their analysis of equid tooth enamel phosphate Bryant et al. (1996a,b–this issue) account for the influence of mother's milk, diet, and seasonal changes in $\delta^{18}O_w$ values on $\delta^{18}O_p$. They conclude that individuals born in the spring are likely to have m1 $\delta^{18}O_p$ values that are higher than those of the other teeth. This is in fact the case for the sheep (Fig. 1), which is known to have been born in the spring. Unlike the sheep, however, the m1 of the bison has a $\delta^{18}O_p$ value that is lower than those of the other teeth (Fig. 1), which is the predicted pattern for animals born in the fall (Bryant et al., 1996a,b–this issue).

4.3. Seasonal changes in $\delta^{18}O_w$ and $\delta^{18}O_p$ values

With the exception of the m1 $\delta^{18}O_p$ values which are influenced by other factors, the tooth enamel data for sheep and bison are a good illustration of the influence seasonal variations have on the $\delta^{18}O_p$ values of hypsodont species. Such variations in local precipitation occur due to changes in local temperature, humidity/evapotranspiration flux, or air mass source in non-tropical areas during the course of a year (e.g. Dansgaard, 1964; Rozanski et al., 1993), and result in lower $\delta^{18}O_w$ values in winter relative to summer. The ingestion of both drinking water and water contained in plants can play an important role in how the sheep and bison record such seasonal variations in $\delta^{18}O_w$.

In the case of the sheep, a cyclic variation in the $\delta^{18}O_p$ values of the m3 samples is mirrored by a trough-like variation of the $\delta^{18}O_p$ values of m2 samples. These intra-tooth variations suggest that the animal periodically ingested water with a relatively low $\delta^{18}O$ value. One possible source of the variation is the drinking water provided to the sheep from a shallow groundwater well. It is unlikely, however, that well waters record seasonal variations in the $\delta^{18}O_w$ (e.g. Wenner et al., 1991), an hypothesis that is supported in part by the fact that seven samples from five different teeth have $\delta^{18}O_p$ values within the narrow range of 0.8‰ (Fig. 1).

A more plausible source of water with low $\delta^{18}O$ values is plant water from grasses that grow in response to winter runoff and spring rains. These grasses will incorporate rain water during their growth and should therefore have $\delta^{18}O_{pw}$ which reflect that of the winter/spring precipitation with a slight positive fractionation. Evapotranspiration effects in arid areas are known to increase $\delta^{18}O_{pw}$ values, but the fact that the spring season is wet, and that the $\delta^{18}O_p$ values of the sheep m1 and m3 are lower than expected, indicate that evapotranspiration did not play a critical role in influencing $\delta^{18}O_{pw}$. The dominant food of sheep in spring is grass, thus the water contained in it should play an important role in influencing $\delta^{18}O_p$ values of its enamel phosphate grown during that period of the year.

The analysis of tooth enamel from wild mammals such as bison involves substantially more unknowns of animal behavior than those that characterize domesticated mammals, particularly with regard to sources of water and food. For example, bison are likely to drink from a variety of water sources such as small streams, ponds, and puddles either as a result of behavior, migration, or simple availability. There is, however, a pronounced cyclic pattern to the $\delta^{18}O_p$ values of the bison m3. Such patterns are strong indications that seasonal changes in $\delta^{18}O_w$ are being preserved in the oxygen of tooth enamel phosphate (Fig. 1). Because all the water sources mentioned have low residence times, this preservation is not unexpected. Rapid volume turnover reduces the effect of evaporation on the $\delta^{18}O$ values of small water bodies, and better allows them to "track" seasonal changes in the $\delta^{18}O_w$ value of precipitation (e.g. Koch et al., 1989).

Plant water was noted to have an effect on the $\delta^{18}O_p$ value of the sheep m2 and m3, and could also have an effect on the $\delta^{18}O_p$ values of the bison m3. If so, the effect does not appear to be random, as a cyclic/seasonal trend in the $\delta^{18}O_p$ values is maintained (Figs. 1 and 2). It is possible that the oxygen isotope composition of plant water may have played a role in attenuating or dampening the seasonal intra-tooth signal in $\delta^{18}O_p$, but the extent of the effect is unknown.

Inter-tooth variation in $\delta^{18}O_p$ values for the bison can also be interpreted as reflecting seasonal changes in the $\delta^{18}O_w$. In the case of sheep, it is argued that the small 0.4‰ difference between premolars is the result of enamel formation that occurs primarily during non-spring seasons when the $\delta^{18}O_{dw}$ value is thought to be relatively constant because the water is supplied to the animals from a uniform reservior. The larger 3.2‰ variation in bison premolar $\delta^{18}O_p$ values, however, implies that the bison was ingesting waters that were influenced by seasonal precipitation *throughout* the year. For a given individual, it appears that a significant amount of inter-tooth variation in $\delta^{18}O_p$ values can occur if the isotopic composition of its drinking water varies seasonally.

Finally, seasonal migration of the bison would effect the enamel $\delta^{18}O_p$ values because these animals ingest water from differing locations throughout the year (although the lack of modern herds of wild bison make it difficult to determine whether bison did indeed migrate in the past; J. Speth, pers. comm.). Typical migrational patterns involve a change in elevation and altitude, where water at high elevations/high latitudes have lower $\delta^{18}O_w$ values than water from low elevations/low latitudes (Dansgaard, 1964; Rozanski et al., 1993). Thus if a bison migrates to lower elevations/altitudes in the winter, it will ingest water with relatively higher $\delta^{18}O_w$ values, the reverse being true with summer migrations to higher elevations/altitudes. The result would be $\delta^{18}O_p$ values that are seasonal, but do not reflect the real climatic conditions of one single location.

4.4. Biology, behavior, and $\delta^{18}O_p$ values

The most important biological factor that will effect the extent to which $\delta^{18}O_p$ values of hypsodont teeth vary in a given environment is the rate of enamel growth. This variable controls the amount of enamel that will form over the course of the seasons, and thus controls the "sensitivity" of $\delta^{18}O_p$ to seasonal variations in $\delta^{18}O$ of ingested water. In addition, the age at which an animal is weaned relative to m1 enamel formation plays an important role in influencing $\delta^{18}O_p$ values. Both of these factors should not be difficult to quantify by analyzing samples from modern populations of a given species, and take them into account when interpreting $\delta^{18}O_p$ data for paleobiological or paleoclimatological research.

More difficult to characterize are behavioral factors that effect $\delta^{18}O_p$, including season of birth and dietary, drinking, and migratory habits. The analysis of enamel from species that are or are not domesticated, that do or do not migrate, that have differing diets, or that have known seasons of birth, however, could provide control groups with which to compare populations collected from archaeological and geological deposits. If the intra-populational variations in $\delta^{18}O_p$ associated with each factor are thus delineated, they will facilitate the characterization and comparison of temporally separate populations for paleoclimatic, as well as paleoecological, research.

4.5. $\delta^{18}O_p$ values as a proxy for seasonality and climate change

The most important paleoclimatic information that can be retrieved from the $\delta^{18}O_p$ values of hypsodont teeth of different ages is the temporal change in the average $\delta^{18}O_w$ value, and the extent of seasonal variations in $\delta^{18}O_w$. Given adequate knowledge of mammalian biology and behavior, specific sampling strategies can be employed to increase the chances of obtaining meaningful information. Any study will require teeth from a number of individuals from each archaeological or geological deposit be sampled so that intra-populational variations in $\delta^{18}O_p$ values can be determined and compared with those from different deposits and a modern analog. In addition, all the sampling should focus on the late-forming premolars or the third molars in order to avoid the isotopic contributions of mother's milk associated with the earliest formed teeth.

The investigation of long-term climate change requires that enamel from temporally separated individuals of the same species form over a similar season. If the individuals are born in the same season, enamel from the cervical margin (Fig. 2) may meet this requirement. This enamel is the last to form, and is likely to have formed during roughly the same interval of a year. Alternatively, $\delta^{18}O_p$ of the smaller teeth, such as the premolars, might prove to be good proxies for $\delta^{18}O_w$ over the short term simply because there is not as much enamel present. Enamel from these teeth will either (1) form at least at the same rate as on the larger molars, in which case the enamel will reflect the $\delta^{18}O_w$ from only a small part of the interval over which a larger tooth forms, or (2) the enamel will form at a slower rate, in which case it will be representative of a longer term average value for $\delta^{18}O_w$. Either way, large amounts of enamel with wide variations in $\delta^{18}O_p$ do not form, thereby reducing the effects of intra-tooth variation associated with larger teeth.

Investigations of seasonality require multiple samples to be taken from single teeth with the greatest crown height, such as the third molar, so that all the variation in $\delta^{18}O_p$ values that occur during enamel formation can be recorded. Seasonality is a measure of the difference in $\delta^{18}O_w$ values between summer and winter in a given location. Assuming $\delta^{18}O_p$ is an accurate relfection of $\delta^{18}O_w$, it can be estimated by measuring the difference between the highest and lowest

$\delta^{18}O_p$ values (Fig. 2). The "average seaonality" for a population can then be compared between samples from different strata to look for an enhancement or reduction of seasonality over time. The analysis of third molars has the additional advantage of providing absolute $\delta^{18}O_p$ values so that longer term changes in the $\delta^{18}O_w$ can be resolved as well as seasonal changes. Both variables are important in the characterization of paleoclimates, and it is a significant advantage of the oxygen isotope technique to obtain information on both from the same archaeological or geological material. The most fruitful paleoclimatic investigations would therefore focus on the analysis and interpretation of samples from the third molar.

Finally, it must be stated again that much of what is described above will only be valid if a mammal is ingesting water with a strong seasonal isotopic signal. For example, groundwater, well water, lake water, and other large reserviors with long residence times, are unlikely to undergo seasonal change in $\delta^{18}O$ values. In this case, the $\delta^{18}O_p$ values would still provide climatic information on decadal or greater timescale fluctuations in oxygen isotope composition of meteoric water, but not on seasonality, season of birth, etc. Similarly, in cases where all the enamel of a tooth is ground up and analyzed, $\delta^{18}O_p$ values should be a reflection of average $\delta^{18}O_w$ values over the time period of enamel growth, and will still be useful in determining long-term climate change.

5. Conclusion

Because large inter- and intra-tooth variations in $\delta^{18}O_p$ can occur in one hysodont tooth, its use as a paleoclimate record is not simply a matter of the random sampling of a given species' teeth through time. The $\delta^{18}O_p$ value of enamel will vary depending on the time of year in which it is formed, the primary source of ingested water, and the species' behavioral habits. As a result, it is important to delineate the effect that these different biological and behavioral factors will have on $\delta^{18}O_p$ values by studying modern populations, and to use this information to characterize sample populations from archaeological and geological deposits. This characterization should provide a more accurate interpretation of $\delta^{18}O_p$ change in relation to climate change. In particular, multiple samples of the large third molars should be able to supply important information on both long-term change in $\delta^{18}O_w$, and on the extent of $\delta^{18}O_w$ seasonality.

Acknowledgements

This research was funded by National Science Foundation grant #EAR9005717. We thank George Frison and Charles Reher for providing access to Vore bison material, Dan Fisher for providing the sheep mandible as well as valuable research suggestions and reviews, Holly Smith and Lois Roe for helpful discussions of mammalian dental development and oxygen isotope systematics, respectively, and Daniel Bryant and Hilary Stuart-Williams for their constructive comments on the manuscript.

References

Ayliffe, L.K., Chivas, A.R. and Leakey, M.G., 1994. The retention of primary oxygen isotope compositions of fossil elephant skeletal phosphate. Geochim. Cosmochim. Acta, 58: 5291–5298.

Brown, W.A.B., Christofferson, D.V.M., Massler, M. and Weiss, M.B., 1960. Postnatal tooth development in cattle. Am. J. Vet. Res., 21(80): 7–34.

Bryant, J.D., Luz, B. and Froelich, P.N., 1994. Oxygen isotopic composition of fossil horse tooth phosphate as a record of continental paleoclimate. Palaeogeogr. Palaeoclimatol. Palaeoecol., 107: 303–316.

Bryant, J.D. and Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochim. Cosmochim. Acta, in press.

Bryant, J.D., Froelich, P.N., Showers W.J. and Genna, B.J., 1996a. A tale of two quarries: Biologic and taphonomic signatures in the oxygen isotopic composition of tooth enamel phosphate from modern and Miocene equids. Palaios, in review.

Bryant, J.D., Froelich, P.N., Showers, W.J. and Genna, B.J., 1996b. Biologic and climatic signals in the oxygen isotopic composition of Eocene – Oligiocene equid enamel phosphate. Palaeogeogr. Palaeoclimatol. Palaeoecol., 176: 75–89.

D'Angela, D. and Longinelli, A., 1990. Oxygen isotopes in living mammal's bone phosphate: Further results. Chem. Geol. (Isot. Geosci. Sect.), 86: 75–82.

Dansgaard, W., 1964. Stable isotopes in precipitation. Tellus, 16: 436–468.

Davis, S.J.M., 1987. The Archaeology of Animals. Yale Univ. Press, New Haven, 224 pp.

Fricke, H.C., O'Neil, J.R. and Lynnerup, N., 1995. Oxygen isotope composition of human tooth enamel from medieval Greenland: Linking climate and society. Geology, in press.

Hillson, S., 1986. Teeth. Cambridge Univ. Press, 376 pp.

Koch, P.L., Fisher, D.C. and Dettman, D., 1989. Oxygen isotope variation in the tusks of extinct proboscideans: A measure of season of death and seasonality. Geology, 17: 515–519.

Levinson, A.A., Luz, B. and Kolodny, Y., 1987. Variations in oxygen isotope compositions of human teeth and urinary stones. Appl. Geochem., 2: 367–371.

Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: A new tool for paleohydrological and paleoclimatological research? Geochim. Cosmochim. Acta, 48: 385–390.

Luz, B., Kolodny, Y. and Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochim. Cosmochim. Acta, 48: 1689–1693.

Luz, B., Cormie, A.B. and Schwarcz, H.P., 1990. Oxygen isotope variations in phosphate of deer bones. Geochim. Cosmochim. Acta, 54: 1723–1728.

O'Neil, J.R., Roe, L.J., Reinhard, E., and Blake, R.E., 1994. A rapid and precise method of oxygen isotope analysis of biogenic phosphate. Isr. J. Earth Sci., 43: 203–212.

Reher, C.A. and Frison, G.C., 1980. The Vore site, 48CK302, a stratified buffalo jump in the Wyoming Black Hills. Plains Anthropol. Mem., 16.

Reinhard, E., De Torres, T. and O'Neil, J.R., 1996. $^{18}O/^{16}O$ ratios of cave bear tooth enamel: A record of climate variability during the Pleistocene. Palaeogeogr. Palaeoclimatol. Palaeoecol., 126: 45–59.

Rozanski, K., Araguás-Araguás, L. and Gonfiantini, R., 1993. Isotopic patterns in modern global precipitation. In: P.K. Swart et al. (Editors), Climate Change in Continental Isotopic Records. Geophys. Monogr., 78: 1–36.

Silver, I.A., 1969. The aging of domestic animals. In: D.R. Brothwell and E.S. Higgs (Editors), Science in Archaeology. Thames and Hudson, London, 2nd ed., pp. 250–268.

Smith, B.H., 1991. Standards of human tooth formation and dental age assessment. In: M.A. Keiky and C.S. Larsen (Editors), Advances in Dental Anthropolgy. Wiley-Liss, New York, pp. 143–168.

Smith, B.H., 1992. Sequence of tooth eruption in primates and other mammals. J. Vertebr. Paleontol., 12(suppl. to 3), p. 52A.

Weinreb, M.M. and Sharav, Y., 1964. Tooth development in sheep. Am. J. Vet. Res., 25: 891–908.

Wenner, D.B., Ketcham, P.D. and Dowd, J.F., 1991. Stable isotopic composition of waters in a small Piedmont watershed. In: H.P. Taylor et al. (Editors), Stable Isotope Geochemistry: A Tribute to Samuel Epstein. Geochem. Soc. Spec. Publ., 3: 195–203.