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Oxygen isotopic determination of climatic variation using phosphate from beaver bone, tooth enamel, and dentine

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Abstract—The $\delta^{18}O$ of Canadian beaver (*Castor canadensis*) teeth should reflect variations in the isotopic composition of the water in which the beavers live, as their incisors grow rapidly and continuously. We observe seasonal variations in phosphate $\delta^{18}O$ using samples of enamel taken along the length of single teeth. In the spring the $\delta^{18}O$ of the enamel being deposited gradually declines, reflecting a retarded input of ^{18}O depleted winter water. After mid-year, enamel $\delta^{18}O$ is higher than average (as represented by the $\delta^{18}O$ of bone phosphate from the same animal) and passes through a maximum in late summer or early fall. Overall, the amplitude of seasonal excursions in enamel $\delta^{18}O$ (4‰) is much smaller than the expected summer-winter range in the $\delta^{18}O$ of meteoric water (>10‰). This is because hydrologic mixing processes, gradual admixing of environmental water with beaver body water, long-term plant growth, and oxygen inputs of relatively constant value (particularly atmospheric oxygen) tend to even out summer-winter differences in the $\delta^{18}O$ of oxygen inputs to the beaver. The $\delta^{18}O$ of bone from adult beavers was uniform at 11.9 ± 0.5‰ over the study area. Analyses of a Sangamon age giant beaver (*Castoroides ohioensis*) incisor from Hopwood Farm, Illinois, show a slightly larger 5.5‰ seasonal cycle of $\delta^{18}O$ with an average enamel $\delta^{18}O$ of 18‰. This suggests that average temperatures were warmer during the Sangamon than today and that seasonal temperature differences and/or relative humidity variations were larger. *Copyright © 1997 Elsevier Science Ltd*

1. INTRODUCTION

The oxygen isotopic composition ($\delta^{18}O$) of biogenic phosphate (δ_p) (including bone phosphate (δ_{pb}) and tooth enamel (δ_{pe})) has been shown to be determined by body temperature and the $\delta^{18}O$ of body water (δ_{bw}) (Longinelli, 1965, 1984; Kolodny et al., 1983; Longinelli and Nuti, 1973; Luz et al., 1984). Mammalian bone is formed at 37°C and is 17.3–17.8‰ enriched in ^{18}O with respect to body water at the time of deposition. The isotopic composition of body water in mammals has been shown to track the isotopic composition of their environmental water (δ_w) although the relationship varies from one species of mammal to another. The principal determinant of δ_{bw} is the $\delta^{18}O$ of local precipitation (δ_{mw}), which varies seasonally and as a function of geographic location (Yurtsever and Gat, 1981), although the isotopic signature may be modified by other mechanisms, primarily evaporation (Ayliffe and Chivas, 1990). The $\delta^{18}O$ of precipitation is strongly controlled by temperature: to a good approximation it follows the relationship $\delta_{mw} = 0.69\ T\ (°C) - 13.6‰$ globally (Dansgaard, 1964), but there is significant local variation. In the study area the relationship is approximately $\delta_{mw} = 0.32\ T\ (°C) - 12.91$ based on data for Simcoe just to the east of the sampled region (Fritz et al., 1987). For herbivores in rather arid areas, relative humidity greatly affects δ_p as it alters the degree to which leaf water in browse is enriched in ^{18}O as a result of stomatal evaporation (Ayliffe and Chivas, 1990; Cormie et al., 1994; Huertas et al., 1995) and also affects the ratio of water lost from the animal as liquid with a composition similar to δ_{bw} vs. water lost as vapour with a substantially lower δ_w than body water. Luz et al. (1990) showed that variation in the δ_{pb} of North American white tail deer could be accounted for by regressing with T and relative humidity (RH) with a correlation coefficient of 0.95. Where δ^2H data are available the relative humidity effect may be refined further (Cormie et al., 1994).

Most studies so far of ancient material have focused on the δ_{pb} of the individual to determine a corresponding average value for palaeotemperature (Ayliffe et al., 1992; Ayliffe et al., 1994; Bryant et al., 1994; Sánchez Chillón et al., 1994) with no examination of how δ_{bw} varies about a mean value. It is also possible to determine shorter-term variations in climate where individual skeletal elements have preserved δ_{bw} during the period of their formation. For example, teeth are mineralized as a mammal grows, and their δ_{pe} is a record of variation in δ_{bw} through the period of growth (Koch et al., 1989; Fricke and O'Neil, 1996; Stuart-Williams and Schwarcz, 1993). More specifically, a rodent's incisors grow throughout the animal's life. Therefore, they can be used as continuous recorders of variation in δ_{bw}. As it is difficult to recognize the effects of low relative humidities in ancient animals (Luz et al., 1990; Cormie et al., 1994), analysis of the δ_p of mammals from humid habitats is preferred. Large aquatic rodents are relatively widespread and their δ_p could be compared with δ_p analyses of rodents from lower humidity environments, such as marmots or rabbits from the same area, to estimate relative humidity. Canadian beaver (*Castor canadensis*) from southern Ontario were selected for this study (Fig. 1) as they live on a moist diet (Novak, 1987), and spend much of their life in the water or in high humidity environments. An ancient beaver, *Castoroides ohioensis,* was also examined for comparative purposes.

2. INTRODUCTION TO BEAVER

Beaver are large, mostly aquatic, rodents of the family Castoridae. The Canadian beaver (*Castor canadensis*) is

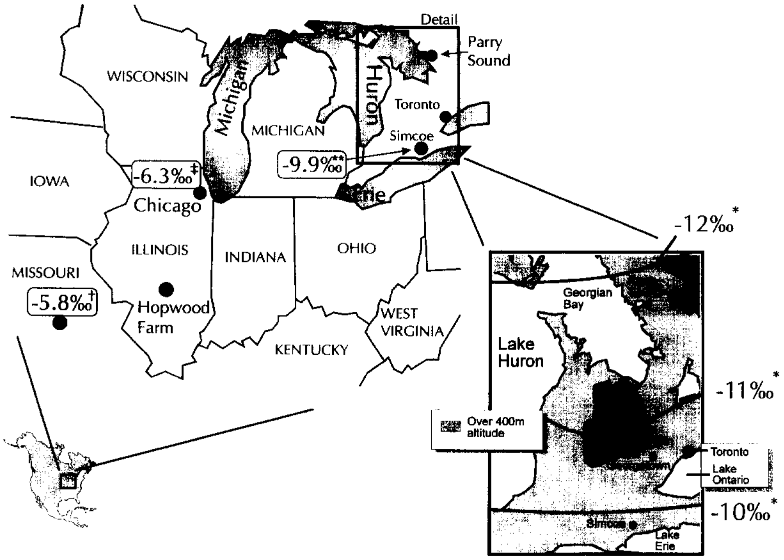

Fig. 1. Location map for samples analyzed. Groundwater δ^{18}O contours* from Fritz et al., 1987; Missouri mean annual $\delta_{mw}{}^{\dagger}$ from Luz et al., 1990; Chicago mean annual $\delta_{mw}{}^{\ddagger}$ and Simcoe mean annual δ_{mw}** from IAEA, 1983.

found in most of nondesert North America south of the arctic tree-line (Novak, 1987). The very similar European beaver (*Castor fiber*) is very widely distributed across Eurasia although it is extinct in some restricted areas, such as Britain where it was exterminated in the Middle Ages (Coles, 1992). Beaver are the largest rodents in North America apart from the capybara (*Hydrochoerus sp.*). Adult beavers weigh 17–40 kg (Novak, 1987) and are up to 1 m in length. These are small in comparison with the giant beaver (*Castoroides ohioensis*) which had an overall length of about 2.5 m and weighed up to 200 kg and which became extinct about 15,000 years ago (Martin, 1967; Martin and Guilday, 1967).

The impact of the beaver on landscapes in temperate zones in the Holocene has probably been significant (Coles, 1992) due to the continual construction, silting, and abandonment of dammed ponds. Breeding usually takes place in the winter with kits produced after the spring thaw in northern areas. The kits stay in the home lodge through one more breeding cycle of the parents but are typically ejected before the next brood is produced. The number of beaver having lodges in a pond is variable, but when food reserves are limited, young beavers will be forced to leave the home area and establish their own colony. Beaver do not hibernate and subsist in winter on the bark of branches stored underwater in the summer and autumn. During the summer the beaver eat more soft vegetable food, including water plants (particularly water lilies) and their roots. Trees are gnawed down in a large area around the pond and canal systems, with branches, twigs, and leaves dragged to the pond to be eaten, added to the food reserve or incorporated into the dam. The fur is waterproof and keeps the beaver dry and warm (Novak, 1987).

3. FACTORS CONTROLLING THE δ^{18}O OF BEAVER INCISORS

Single *Castor* incisors record δ_p variations over two to four months (depending on the rate of wear of the teeth; Stuart-Williams and Schwarcz, 1993). By assembling data from a number of individuals in a given region we can reconstruct the seasonal cycle in δ_{bw} and from that infer something about seasonal variation of δ_{mw} in the region.

The overall oxygen budget of a beaver is shown schematically in Fig. 2. As with all animals the δ_{bw} of beaver is determined by the balance between inputs and outputs of oxygen. The principal inputs are drinking water, food, and atmospheric oxygen. The first two are both strongly coupled to the δ_w of the pond in which the beaver lives. Beavers eat bark, roots, shoots, and leaves, which may include both new growth, and old growth whose isotopic composition represents an average δ_w over a year or more. The precise relationship between δ_{bw} and δ_w for beavers has not yet been determined, but is presumed to be of the form

$$\delta_{bw} = A\delta_w + B$$

where B is an offset of the order of magnitude of 5‰, and A is the so-called metabolic slope (MS). The value of A is typically <1.0 because body water includes a component of metabolic water (from oxidation of nutrients; D'Angela and Longinelli, 1990) where the δ^{18}O of atmospheric oxygen is fixed at approximately 23.5‰, although a small negative offset (-2 to -9‰) is produced by kinetic processes during the uptake of oxygen from the air (Bryant and Froelich, 1995). The food itself also contains oxygen, for example in carbohydrates. Leaf water in plants is typically fractionated by 10–25‰ in ^{18}O when compared with their environment (Dongmann et al., 1974 and references in Bryant and Froelich, 1995; in high humidity settings or aquatic plants the fractionation is probably less) while the cellulose is fractionated by about 27‰ relative to the leaf water (Epstein et al., 1977 and references in Bryant and Froelich, 1995). Ideally we would determine the metabolic slope and offset by comparing δ_{pb} and δ_{mw} for beavers from a wide geographic range, to maximize the spread in δ_{mw}. The present study was carried

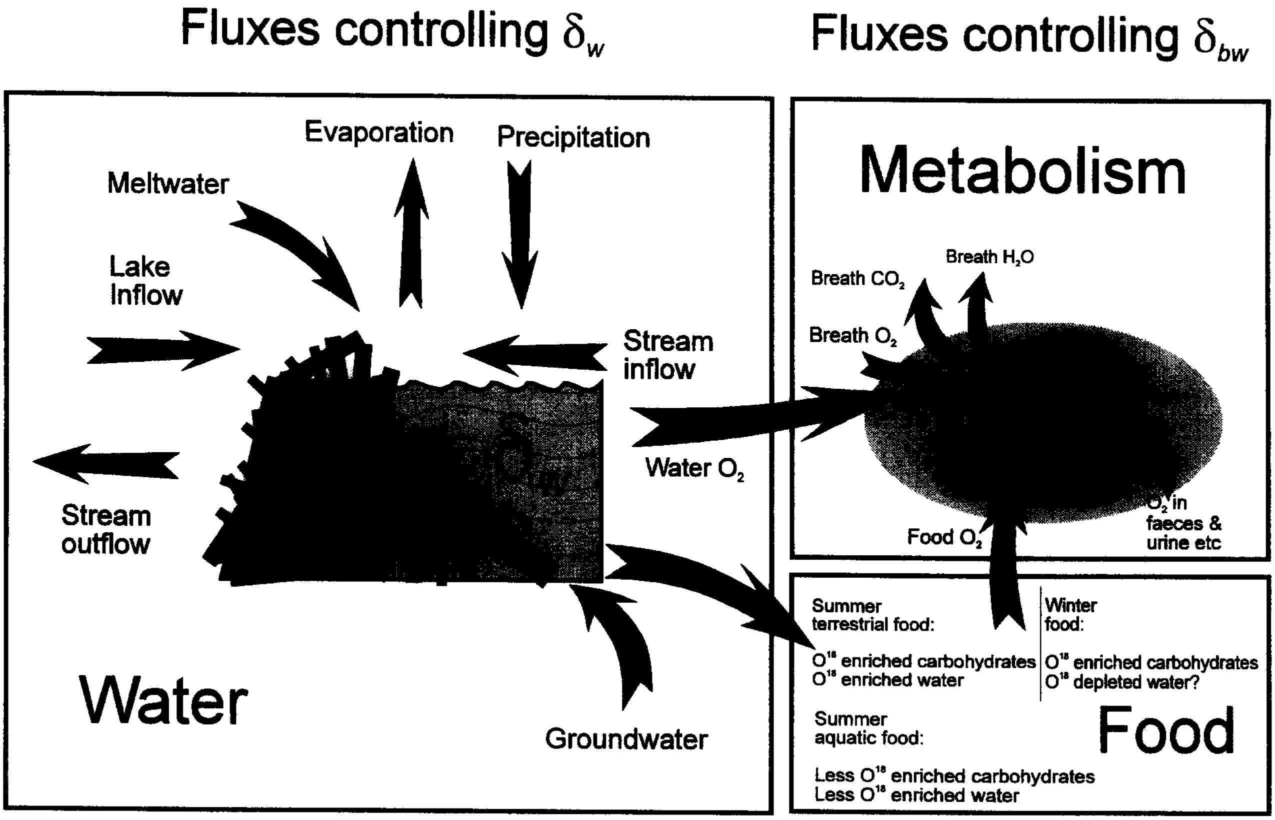

Fig. 2. The liquid water oxygen influx in a beaver is particularly subject to local variability which is summarized in the left box. Dietary oxygen isotopic influences are summarized in the lower right box. The beaver's metabolic fluxes (upper right box) then act within the context of these major inputs.

out in Southern Ontario where there is apparently little variation in mean δ_w, so that it was not possible to determine values of A and B by regression of δ_{bw} against δ_w. Nevertheless, we can use the δ_p of tooth enamel to obtain some knowledge of short-term variations in environmental water. Typically (Bryant and Froelich, 1995 and references therein) values of A for kilogram-sized mammals are of the order of 0.6–0.9, so a change of 1‰ in δ_w should result in a change of the order of 0.6–0.9‰ in tooth enamel deposited at that time.

Changes in δ_w are broadly controlled by seasonal variation in δ_{mw}. For the Southern Ontario region, δ_{mw} varies cyclically between a summer maximum and a winter minimum, as shown by IAEA records of precipitation at Chicago, Simcoe (close to the collecting sites), and Ottawa (Fig. 3a; IAEA, 1969, 1970, 1983). δ_{mw} averaged from 1976 through 1979 at Simcoe varies from about −19‰ in winter to −6‰ in summer, although there is substantial variation, particularly in winter values, from year to year (Fig. 3b). There should be an analogous annual cyclicity in the isotopic composition of freshly deposited tooth enamel, as the beaver's internal water pool responds to changes in δ_w triggered by changes in δ_{mw}. The seasonal signal recorded in the enamel may, however, differ markedly in form, phase, and amplitude from seasonal changes in δ_{mw} near the living site of the beaver. The principal factors determining the interaction between δ_{mw}, δ_w, and δ_{bw} are discussed below.

3.1. Variations in the $\delta^{18}O$ of Surface Water

Much of the water consumed by the beaver directly, or indirectly through vegetation, is derived from the pond or river in which the beaver lives. The isotopic composition of this water is in turn determined by the balance between inputs (principally surface runoff and groundwater discharge) and outputs (outflow and evaporation). Of these, only evaporation leads to isotopic fractionation, causing $\delta^{18}O$ to increase in the summer when evaporation rates increase. Due to periodic warm periods, snow-cover is not extensive and does not remain through the winter in most of the study area. As a result of this there is only a small direct contribution of low-$\delta^{18}O$ melt water to the ponds and streams in the spring.

The water level in the pond or river is maintained by groundwater discharge, which will tend to dampen the seasonal oscillations of $\delta^{18}O$ as the mixing of meteoric water with a larger reservoir of groundwater will result in a reduced amplitude of seasonal δ_w variation and cause the δ_w signal to lag behind changing δ_{mw} (Fig. 4). If the water of the ponds represents inputs integrated over 6 months (due to groundwater mixing and the capacity of the pond and stream) then the amplitude of δ_w variation in the Simcoe area is reduced to 5‰ and δ_w reaches a maximum in September, 2 months after the δ_{mw} maximum. Both a reduced range of $\delta^{18}O$ variation (when compared with the annual range of

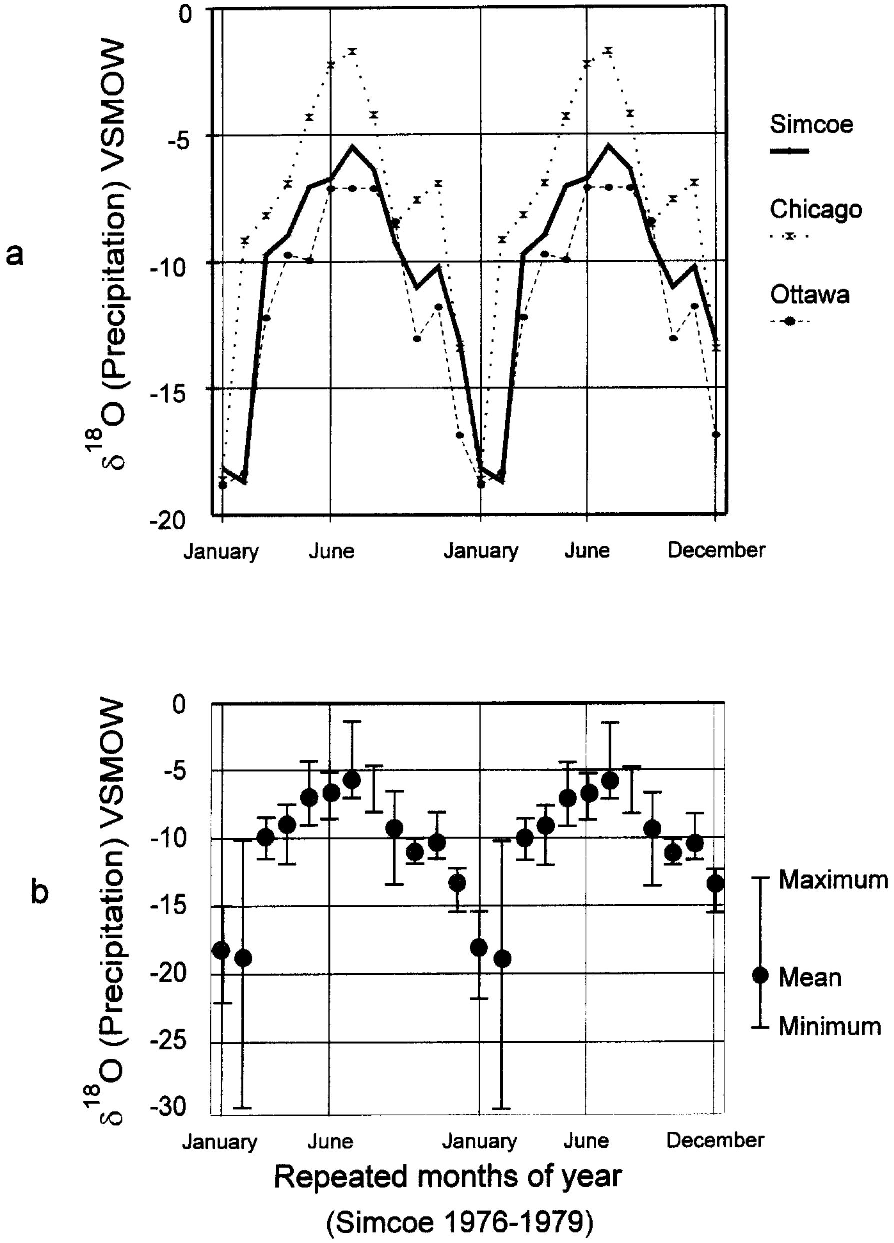

Fig. 3. (a) The δ^{18}O of precipitation at Chicago (Illinois), Ottawa, and Simcoe (Ontario). The unweighted data are averaged over four years (1976–1979) and are repeated to emphasize the pattern of the annual variation. (b) Annual variation in the δ^{18}O of precipitation at Simcoe, Ontario. Greater variability is found in the drier winter months. In general the lowest isotopic values are associated with colder winters and less precipitation, perhaps due to cold, dry arctic air masses. (IAEA, 1983)

δ_{mw}) and a delayed response are expected in the isotopic records of beaver tooth enamel (Fig. 4), although part of the reduced range must result from a metabolic slope of <1.

3.2. Vegetation

Beaver obtain some of their body water from the consumption of woody vegetation, resulting in further damping of seasonal oscillation in δ^{18}O because woody plants integrate the variation in δ_{mw}.

3.3. Geographic Location

There is about 2‰ variation in the δ_w of groundwater over the study region (Fritz et al., 1987), which is slightly greater than the 1.5‰ expected range of mean annual δ_{mw} (from Parry Sound to Georgetown; Luz et al., 1990; Fig. 1). Also, we recognize that some of the beaver taken at sites near to Georgian Bay could have been living in inlets influenced by Lake Huron water which is expected to be significantly less seasonally variable in δ^{18}O than smaller water bodies.

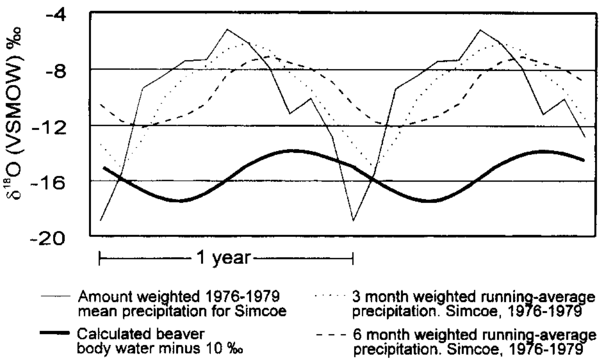

Fig. 4. Phase shifts in $\delta^{18}O$ responses of the beaver and its environment as a possible result of the mixing of existing oxygen in plants, surface water, and groundwater with recent precipitation. The composition of the beavers' body water (which is displayed as an approximate copy of the form of the LOWESS fit of tooth enamel analyses in Fig. 5e) lags behind the isotopic composition of the precipitation and approximately matches a six month running-average of amount-weighted precipitation $\delta^{18}O$.

4. SAMPLES

Sixteen beaver heads were obtained in 1993 and 1994 from trappers killing them either for pest control or for their pelts. Because the fur is not usable in the summer we obtained no specimens from June through September in either year. All samples come from southern Ontario: from around Parry Sound at the east end of Lake Huron and from Georgetown and Erin west of Lake Ontario (Fig. 1, Table 1). Parry Sound is on the edge of the Laurentian shield which in this area comprises a suite of glaciated, impermeable Precambrian metasediments and igneous rock with water trapped on the surface. Georgetown and Erin are situated on Silurian and Upper Ordovician dolostones and shales which are mostly well drained except where the surface water is captured as marshes and kettles by thick periglacial deposits. Exact kill sites were not provided by the trappers so it is not possible to correlate δ_p exactly with environmental controls. The Erin beaver were obtained from the Ontario Ministry of Natural Resources and were not originally acquired for this study. The month of death for all the beavers was recorded by the trappers. Some of the Parry Sound beavers had the roots of the incisors cut off when the jaw was removed by the trapper. In a few of these cases small amounts of enamel were lost and the size of the missing portion was approximated from comparison with other teeth and jaws. Neither the sex nor the body mass of the beavers could be determined.

The beavers were divided into three groups on the basis of the width of the lower incisors. Adults have lower incisors ≥ 7 mm wide, yearlings have incisors from 5–7 mm wide, and young beaver incisors are ≤ 5 mm wide. A total of ninety-five samples from beavers of all ages was used for this survey (Table 1).

Left or right lower incisors were sampled every 20 mm from the tip (Fig. 5a,b) apart from the initial study in which EBA 1 and EBA 2 were sampled every 5 mm (Stuart-Williams and Schwarcz, 1993). Approximately 15 mg samples of enamel were ground as a strip across the front of the tooth using a diamond burr, starting at the occlusal end. In an adult beaver about 2 cm of the incisor at the root is very thin walled, and enamel is absent. Above this for about 1.5 cm toward the tip the enamel is very spongy and contains a great deal of organic material. The portion of the tooth toward the occlusal surface from this is evenly coated with hard enamel. While every effort was made to grind off only enamel, minor amounts of dentine may have been included. As some seasonal variation is probably also present in the dentine, we used ~50 mg samples of bone from the back of the jaw of each beaver to obtain an average δ_{bw}.

A giant beaver (*Castoroides ohioensis*) lower incisor from the Hopwood Farm locality (King and Saunders, 1986; Blackwell et al., 1997; Fig. 5c,d) was kindly provided by the Illinois State Museum. The tooth comes from a buried kettle depression filled with Sangamonian interglacial deposits (Blackwell et al., 1997) of gytjja (aqueous sediment with a high proportion of organic material), fossiliferous silty clay, alluvium, and loess resting on scoured Illinoian till. The beaver incisor sampled rested above a mastoturbated

Table 1. Sample information for beaver in this study.

ID	Sample part	Length × width (cm)	Month	Yr	Place	No. samples
TL1	Left l. incisor	12.0 × 0.63	4/5	94	Parry Sound	5
TL2	Right l. incisor	12.5 × 0.7	4/5	94	Parry Sound	5
TL3	Right l. incisor	12.0 × 0.75	1	94	Parry Sound	5
TL4	R. l. inc. No root	7.0 × 0.5	1	94	Parry Sound	5
TL5	L. l. inc. No root	7.7 × 0.7	12	93	Parry Sound	4
TL6	L. l. inc. No root	8.5 × 0.7	12	93	Parry Sound	4
TL7	L. l. inc. No root	7.0 × 0.5	2	94	Parry Sound	3
TL8	L. l. inc. No root	12.0 × 0.7	2	94	Parry Sound	5
EBA1	Lower incisor	11.0 × 0.7	5	93	Erin	7
EBA2	Lower incisor	11.0 × 0.7	5	93	Erin	16
EB2	Left l. incisor	8.5 × 0.5	1	93	Erin	3
GT1	Right l. incisor	8.7 × 0.45	10/11	94	Georgetown	3
GT2	Right l. incisor	8.5 × 0.45	10/11	94	Georgetown	3
GT3	Right l. incisor	12.5 × 0.73	10/11	94	Georgetown	5
GT4	Right l. incisor	11.0 × 0.65	10/11	94	Georgetown	5
GT14	Right l. incisor	12.5 × 0.8	10/11	94	Georgetown	5

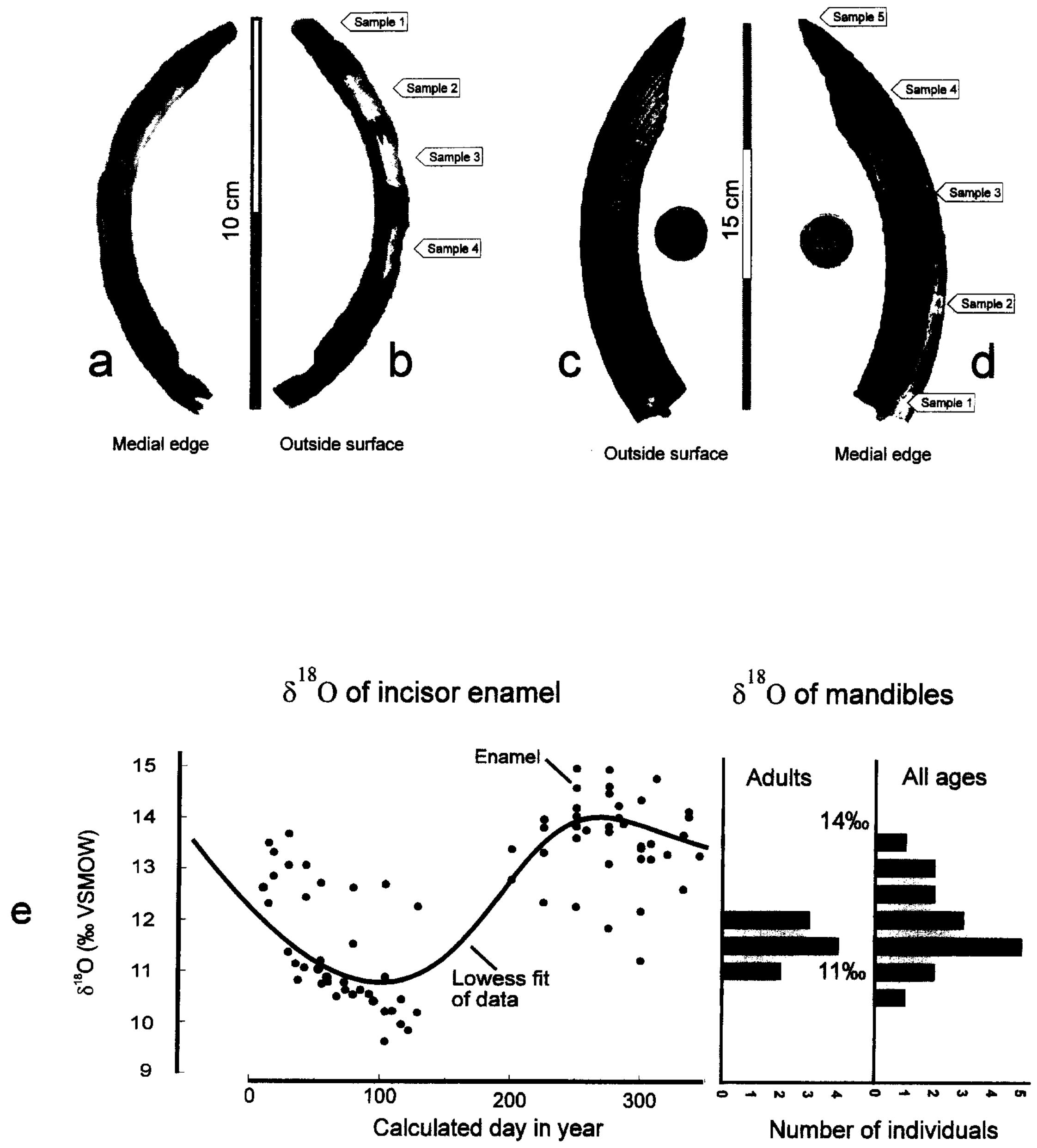

Fig. 5. (a–d) Sampled beaver incisors. The modern beaver (*Castor*) lower incisors (a,b) were sampled by grinding across the tooth whilst the giant beaver (*Castoroides*) tooth (c,d) was sampled by the removal of small rectangles of enamel from the inner edge. (e) Tooth enamel and jawbone analyses of the specimens. Enamel values are displayed as dots. A locally weighted regression (LOWESS) fit of the enamel data is shown for comparison with the curves in Fig. 4 above. The abscissa was calculated by assuming a growth rate for the teeth of 0.75 mm day^{-1}. The two histograms on the right, at the same vertical scale as the enamel analyses, show the frequency distribution for isotopic analyses of the beaver mandibles. Values from adult beavers only (left histogram) are more tightly clustered than when data from young beavers are included (right histogram).

horizon at the base of stratum 2 with *Mammut americanum* (mastodont) remains, *Trionyx sp.* (soft-shelled turtle), *Castor sp.*, and a variety of other bones (Blackwell et al., 1997). The layer immediately below (stratum 3) includes a fauna of *Lepistosteus platostomus* (shortnosed gar) and *Geochelone crassiscutata* (giant tortoise). Pollen is absent from stratum 2 but is present in stratum 3 below and indicates few *Picea* and *Pinus* trees with increasing amounts of *Quercus, Ulmus, Carya, Poaceae,* and *Ambrosia* and greatly decreasing amounts of *Chenopodiaceae* (King and Saunders, 1986), perhaps suggesting a preponderance of open deciduous woodland in Stratum 2. The tooth was complete apart from a 29 mm length sawn from the base for electron spin resonance dating, yielding dates of 33–86 ka depending on the uranium uptake model used (Blackwell et al., 1997). A mastodont molar analyzed from the same horizon was ESR dated at 71–122 ka. The difference between the dates is due to either dating problems or allochthony of the samples (Blackwell et al., 1997). Five samples of about 20 mg were ground as elongated rectangles parallel with the length of the tooth. This caused a reduction in time resolution but was less disfiguring to the specimen than grinding the enamel transversely. Averaged δ_{bw} was determined from 80 mg of dentine from the interior of the sawn end.

5. ANALYTICAL PROCEDURE

Approximately 15 mg enamel samples from specimens apart from Beavers EBA 1 and EBA 2 were processed using a lead phosphate/lead sulphate/Ag_3PO_4 method (Firsching, 1961; H. Le Q. Stuart-Williams and H. P. Schwarcz, 1997). The silver phosphate produced was reacted with bromine at high temperatures (Stuart-Williams and Schwarcz, 1995). Beavers EBA 1 and EBA 2 were processed in a similar manner except that after oxidation of organic compounds the phosphate was precipitated as $Ba_3(PO_4)_2$ which was converted to silver phosphate and reacted with BrF_5 for 18 h (Tudge, 1960; Crowson et al., 1991). Liberated oxygen was converted to CO_2 by heating with a carbon rod and analyzed using a VG 602 or a VG SIRA isotope ratio mass spectrometer. The total standard deviation of analysis of all samples is about 0.15‰. The analyses used in this study are presented in an Appendix. Only two duplicates were run because of the limited amount of isotopically similar sample available. The differences between the analyses were 0.14‰ and 0.03‰. Analysis of inorganic phosphate using these techniques has a 1σ precision of ±0.13‰. All results are presented relative to the VSMOW standard and include corrections for the offset induced by the bromine reaction.

6. RESULTS

Figure 5e shows the data for all tooth enamel samples as a function of the estimated date of deposition of each enamel sample. The dates are assigned assuming a constant growth rate of 0.75 mm day and from knowledge of the date of kill; the growth rate estimate is discussed below. The δ_{pb} of the associated jaw bones is also shown, which is presumed to represent the long-term average value of δ_p. A LOWESS (locally weighted regression) curve has been fitted to the enamel data, to give some idea of the overall seasonal variation in δ_{pe}. Oxygen isotopic profiles from each tooth are shown in Fig. 6a.

In general, we observe a trend of decreasing δ_{pe} early in the year. When the record picks up again in the fall (after the absent summer samples), δ_{pe} has sharply risen by 2–3‰. From late summer onwards, the data show a gradual rise followed by a decrease into the winter. Overall, this trend resembles the seasonal pattern of δ_{mw}, but there is a considerable lag. This is especially marked by the continual decrease in δ_{pe} in the spring, whereas local δ_{mw} would be expected to rise by mid-January or February.

The δ_{pb} of jawbones lie "in general" close to the annual mean values for δ_{pe} as expected if δ_{pe} or δ_{pb} are not unequally influenced by growing season values (Fig. 5e), but there are some exceptions to this rule, to be discussed below.

δ_{pe} for *Castoroides* ranges from 15.4–20.4‰ and the $\delta^{18}O$ of the dentine is 18.7‰ which is 0.8‰ greater than the median δ_{pe} of 17.9‰.

7. TOOTH GROWTH RATE ESTIMATION

Only the enamel deposited at the base of the incisor immediately before death can be dated precisely. The remaining samples are relatively dated, using an estimated growth rate for the incisor. The rate of growth can be constrained in several ways: (a) matching the isotopic data to seasonal fluctuations; (b) using small marks on the sides of the teeth which may be growth lines; and (c) relating changing skull and tooth sizes in immature beavers. (a) Beavers EBA 1 and EBA 2 both showed monotonically decreasing values for δ_{pe} with time (Fig. 6a), apparently representing only a part of the year when δ_{bw} was decreasing from the high summer values. This showed that the entire incisor was cycled in less than about 8 months before the beginning of May kill date, representing a minimum tooth growth rate of 0.7 mm day^{-1}. In the EBA beavers the highest δ_{pe} was similar to their jawbone δ_{pb}. In mature beaver δ_{pb} is expected to be similar to the weighted annual mean value of δ_{pe}. The δ_{pe} recorded, which is all isotopically lighter than δ_{pb}, is, therefore, unlikely to represent more than 6 months of deposition at a growth rate of perhaps 1 mm day^{-1} or more. (b) Fine lines with a spacing of 0.65–0.8 mm, perhaps daily growth lines, are present on the sides of adult teeth. (c) Our data indicate that juvenile beaver teeth are about 4.5 mm wide by October of the beaver's first year. The width has increased to about 5 mm by January or February of the following year and to 7 mm by the end of the next summer, when further increase in width becomes substantially slower. The taper along the length of the juvenile incisors is about 0.5–1.0 mm, and the 85 mm long teeth have, therefore, been completely used up by wear about three times in a year, at a growth rate of about 0.75 mm day^{-1}.

We have, therefore, used an estimated growth rate of 0.75 mm day^{-1} when graphing the data. This is more probably an underestimate than an overestimate as analysis of other beavers in the study has shown that adult beaver killed in December may already retain no trace of δ_{pe} increasing through the summer. In the cases of beavers GT 3, GT 4, and TL 5, a growth rate of 0.75 mm day^{-1} is difficult to reconcile with an interpretation of isotopic seasonality as discussed below and a growth rate of 1.2 mm day^{-1} was used for some graphs.

No comparable growth lines were visible on the giant beaver tooth, but as they are very superficial features in *Castor* they could have been destroyed during burial. More than a complete annual cycle of $\delta^{18}O$ variation appears to be visible in the tooth and the growth rate was about 15 cm $year^{-1}$, or about 0.4 mm day^{-1} (Fig. 7).

8. DISCUSSION

8.1. Consistency of Data

The sequential analyses within teeth define continuous, smooth trends that track gradual variation in the ^{18}O fluxes, particularly seasonal variation in δ_w. For example, we note the two beavers EBA 1 and EBA 2 which were collected from the same pond and which have closely matched records which both show a gradual drop in δ_{pe} through the early spring. The agreement between successive samples along the growing teeth is consistent with our estimate of analytical reproducibility of ±0.15‰. These data give confidence in the reliability of analyses of single teeth from other sites.

8.2. Seasonal Trends in δ_{pe}

Decreasing δ_{pe} through the spring and the delay of increasing δ_{pe} until the summer suggest that throughout this sam-

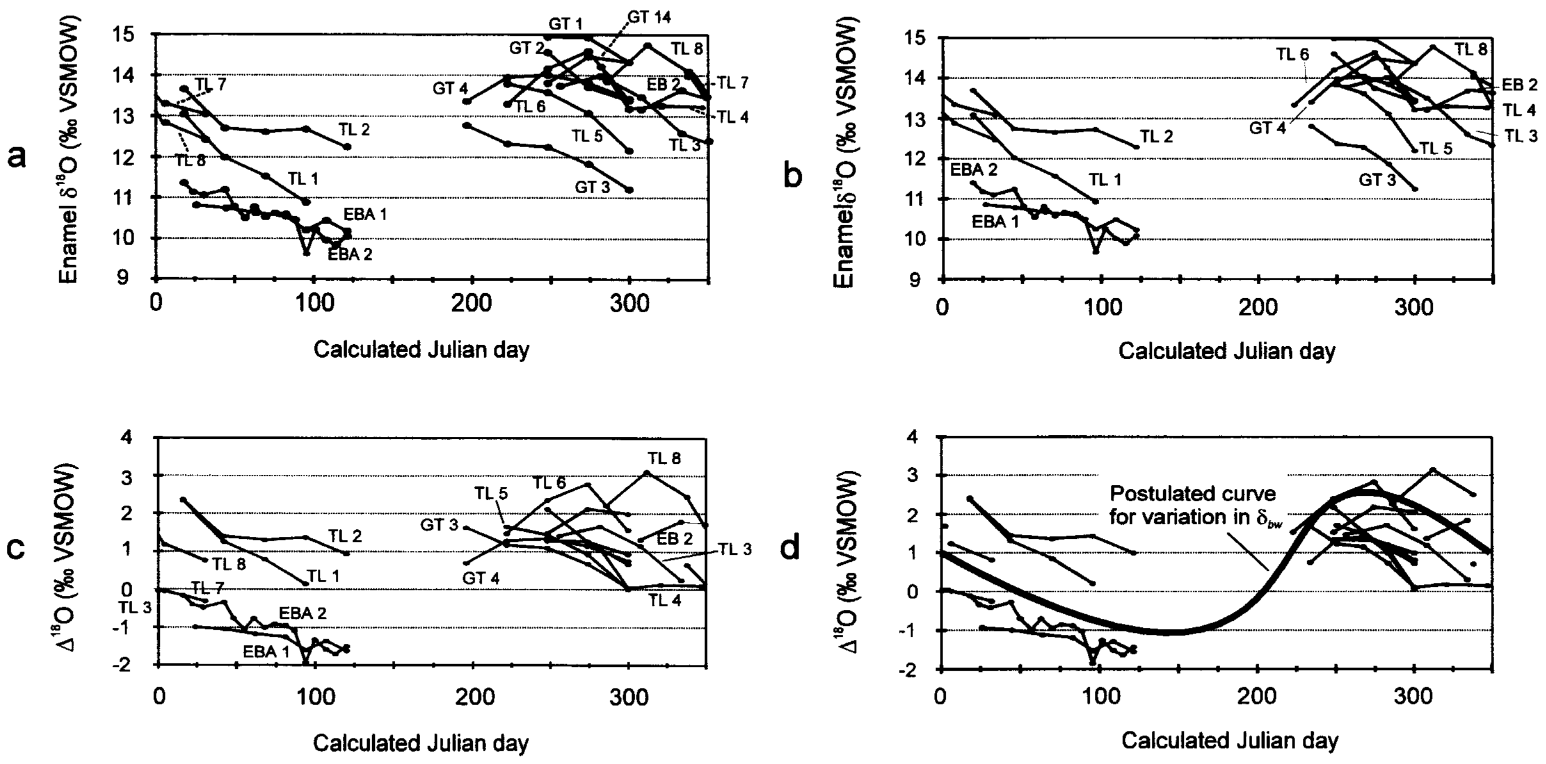

Fig. 6. Profiles for *Castor* δ_{pe}. (a) Data from analyses of incisor enamel with an estimated tooth growth rate of 0.75 mm day^{-1}. Records from beavers killed early in the year are wrapped around to the end of the year, for example beavers Tl 7 and TL 8. (b) As in (a) but with growth rates for GT 3, GT 4 and TL 5 increased to 1.2 mm day^{-1}. (c) As in (a) but with δ_{pe} values converted to offsets from δ_{ph} ($\Delta_{(\delta pe-\delta pb)}$). (c) Data with modified tooth growth rates as in (b) above but converted to offsets from δ_{pb} as in (c) above.

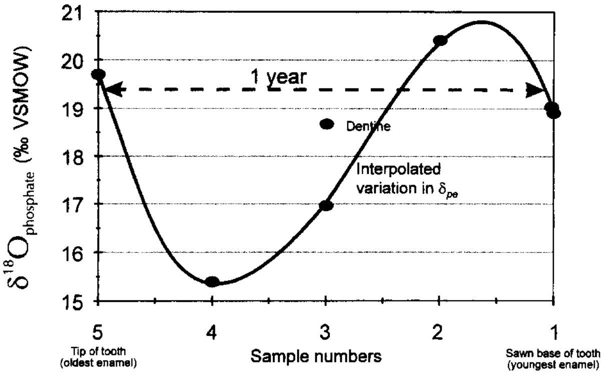

Fig. 7. Oxygen isotopic analyses of a giant beaver (*Castoroides ohioensis*) lower incisor from Hopwood Farm, Illinois. Slightly more than one year is probably represented by the samples which appear to show an isotopic cyclicity similar to that found in modern Canadian beavers.

pling region there is a tendency for δ_w to lag behind δ_{mw}. Possible reasons for this were presented earlier, principally mixing of recent precipitation with the large reservoir of groundwater. A similar effect in delayed rise of δ_w has been observed in Dutch rivers by Mook (1970) where there is a significant contribution of snow melt from the Alps. Snow cover is usually neither extensive nor persistent in the study region, but perhaps a high proportion of the moisture from snow from December through February is trapped in the frozen soil until temperatures are consistently above freezing, beginning in late March (day 80).

Although we have no data for late spring and summer, it is clear that there must be a very rapid rise in δ_{pe} during this period, in order to account for the high values recorded in the early fall. The rapidity of rise is similar to that observed in the δ_{mw} record (Fig. 3a), but it is not clear whether δ_{pe} would track δ_{mw} more closely (with a very much smaller time lag) in the absence of a snow melt effect.

Data for teeth collected in the fall show remarkable variability in their trends. Some show continuous decrease (GT 3 and TL 5) while in others δ_{pe} rises and then falls, reaching its maximum at dates which vary over a span of almost two months. These presumably record the vagaries of the balance between delayed summer runoff, local evaporation rates from pond surfaces, and delayed utilisation of vegetation which has grown from ^{18}O-enriched waters present during the height of the growing season. The lowest values and generally decreasing trends in δ_{pe} obtained for beavers caught in late fall are continuous with the trends observed in spring-caught beavers, showing that there is a steadily decreasing trend in the $\delta^{18}O$ of the water available to the beavers from late fall to mid spring.

The variation in overall δ_{pe} between beavers caught at the same time in a small area is very large. For example, apparently coeval enamel laid down by beavers collected at Georgetown varies by more than 3‰, although most of the spread results from the anomalously ^{18}O depleted specimen GT 3. Since beavers seldom change ponds, this indicates that the local variability of δ_w in the beaver's environment is a large fraction of the total variability over the entire region of southern Ontario sampled in this study. This again reflects the vagaries of local hydrology, evaporation rates, recharge rates, etc., and places some limits on the degree to which we can expect the δ_{pe} of a single beaver sample to represent regional palaeoclimate. In addition, when δ_{mw} is instantaneously sampled like this, it should be noted that even weighted mean annual δ_{mw} can vary by 2‰ from year to year (IAEA, 1983).

8.3. Regional Trends

As noted above, there is a gradient of increasing δ_{mw} across the study area as interpolated from the known continent-wide trends (Cormie, 1991). This is reflected in an approximately 2‰ increase in groundwater δ_w southward over the study area (Fritz et al., 1987) and, presumably, also in the surface waters which are recharged by a combination of runoff and groundwater. There does not seem to be any corresponding trend in δ_{pe} across the region. On the contrary, samples from the northernmost collection area (Parry Sound: samples TL 3–8) have, on the average, higher δ_{pe} values than those from the more southerly Georgetown sites. This may be due to higher evaporation losses and less groundwater recharge affecting the water bodies in which the Parry Sound Beavers lived.

8.4. Amplitude of Seasonal Variation

Whereas the general seasonal trend in the $\delta^{18}O$ of tooth enamel is as expected from the form of its driving function (δ_{mw}), the amplitude of the cycle is substantially lower. The LOWESS curve varies by about 3‰ while the maximum amplitude of seasonal variation at a given site is about 3.6‰ (at Parry Sound). By contrast, the seasonal variation in weighted monthly average δ_{mw} at Simcoe is about 13.5‰ (IAEA, 1983).

Part of the reduction in amplitude of the seasonal cycle of δ_{pe} is due to the metabolic slope coefficient, A, in Eqn. 1 probably being less than unity. In order for a large part of the reduction in amplitude to be due to this source, however, the value of A would have to be unacceptably small (c. $3/13 = 0.23$). This is smaller than metabolic slopes reported for desert animals which recycle a large part of their metabolic water (e.g., *Equus burchelli*, $A = 0.29$; Bryant and Froelich, 1995). Furthermore, beavers may consume vegetable foods in the summer (leaves and grasses) which have been substantially enriched in ^{18}O by evaporation and which could tend to increase δ_{bw} in summer and increase the total amplitude of seasonal δ_{bw} fluctuation. Therefore, we cannot attribute the whole of the damping of the δ_{pe} signal to the role of metabolic water in beaver body water, although this is probably a contributing factor and the total influence of varying metabolic rate and metabolically derived water remains uncertain.

The major part of the reduction in amplitude must be due to the factors cited above: blending of runoff, groundwater, and surface waterbodies, contribution of metabolic water derived from bark and some woody vegetation (whose $\delta^{18}O$ values are themselves seasonal averages), and the mixing of oxygen influxes with the beaver's own body water pool over a period of time. Identification of the factors controlling damping at any given locality would require knowledge of the specific living site of a given beaver. It is significant that the damping is seen in all the beavers sampled, showing that this is a general, regional effect that is apparently produced by variable contributions from a number of sources which, on the average, result in approximately the same degree of damping of the δ_{mw} signal.

In some beavers (e.g., GT 3, GT 4, and TL 5) δ_{pe} begins to decrease between day 200 and day 250, while other beavers (e.g., TL 3 and TL 6) show increasing values until past day 275. Beaver TL 8 still shows increasing values after day 300. When the change to decreasing δ_{pe} occurs later in the year it is usually associated with higher δ_{pe} so that in Fig. 6a the profiles appear to be stacking up and to the right, as though some ponds have continued to evaporatively fractionate or have not been diluted by groundwater until later in the year. This effect is found both in the Parry Sound beavers and the Georgetown beavers and is a significant contributor to scatter within groups of beavers from a site. Indeed three beavers collected at Georgetown were apparently simultaneously depositing phosphate that differed in isotopic composition by more than 3‰.

Beaver GT 3 shows decreasing δ_{pe} very early, by day 200. This may partly result from hydrologic influences, but the lower slopes and unreasonably early autumn inflections on GT 3 and TL 5 could be accounted for by a very high incisor growth rate. By contrast, the largest beaver, GT 14, shows increasing δ_{pe} later in the year than any of the other beavers. An arbitrarily accelerated growth rate of 1.2 mm day^{-1} has been applied to GT 3, GT 4, and TL 5 in Fig. 6b, which is otherwise identical to Fig. 6a. This lessens the phase differences between these teeth and the others. GT 4 may differ in response because it is a yearling. Young beaver are tolerated in the home pond for varying amounts of time, depending on, among other factors, pressure on available food supplies. They are then forced by the parents to leave and establish new territory and build their own dams and lodges (Novak, 1987). This may happen in their second year or at any point thereafter. The three beavers with the apparently accelerated tooth growth may have been living in less well dammed water which was less stagnant and less $\delta^{18}O$ enriched by evaporation, and they may have worked their teeth down more rapidly building new dams. This explanation certainly matches the Georgetown samples which were killed as part of a pest control program: new colonies are more likely to be selected for extermination.

8.5. Relation to $\delta^{18}O$ of Bone

As might be expected, the jawbone $\delta^{18}O$ (δ_{pb}) of adult animals is close to the median value of δ_{pe} for the same beaver (Fig. 5e). That is, the jawbone, which has grown throughout the animal's life, records an average value of δ_p, whereas enamel records quasi-instantaneous values for accreting apatite. We would also expect that the difference $\Delta_{eb} = \delta_{pe} - \delta_{pb}$ would at any given time be more uniform across the region than the δ_{pe} values themselves, because this difference would represent the seasonal component of variation and would compensate to some extent for local differences in the base level of δ_w. Figure 6c shows values of Δ_{eb} vs. date for all the teeth in this study. As expected, we observe less variation in Δ_{eb} at a site through the year than was found in δ_{pe}. Figure 6d is similar, except that the growth rates of some teeth are accelerated as in Fig. 6b.

One group of teeth appears anomalous, however. The spring values for TL 1, TL 2, TL 7, and TL 8 are all significantly higher than δ_{pb} for each animal, as is shown by the positive Δ_{eb} values recorded between days 0 and 100. Beaver TL 7 is a juvenile and because the jawbone is still growing, its composition is close to that of the enamel. This is typical of young animals where bone remodelling is so rapid that Δ_{eb} is often small or anomalous when compared with adult beaver. The remaining three beavers in the group show δ_{pe} values considerably greater than δ_{pb}, although it is expected that δ_{pb} should be greater than δ_{pe} in the spring. There are several possible explanations for the anomalous results, including an unusually late minimum δ_{mw} at this location in 1994; a smaller than usual input of winter precipitation; unusual weather patterns (such as Pacific rather than Atlantic air-masses dominating) or an exceptionally warm winter (with unusually high δ_{mw}). By contrast, beavers from elsewhere in Ontario (EBA 1 and 2) give Δ_{eb} values that are approximately symmetric around zero.

The range in Δ_{eb} over the entire dataset is approximately 4‰, which is not significantly different from the variation in the δ_{pe} data themselves. This suggests that most of the variation in the $\delta^{18}O$ of bone apatite is due to region-wide seasonal shifts in δ_w (and indirectly, δ_{mw}) rather than to the regional trend in δ_w.

9. VARIATION IN THE $\delta^{18}O$ OF ENAMEL OF A *CASTOROIDES* INCISOR

The data for the Hopwood Farm, central Illinois, sample of *Castoroides* are presented in Fig. 7. A smooth curve representing the hypothetical seasonal variation has been drawn through the five data points with a range of δ_{pe} from 15.4 to 20.4‰. The single analysis of dentine for this individual lies near the median of the enamel data, as expected for bone, although this may be coincidental as the dentine probably also varies cyclically in composition. The seasonal curve data suggest that the extant portion of this tooth grew over a span of approximately one year. The estimated continuation of the curve between the data points suggests that the maximum amplitude of variation in δ_{pe} was not much greater than that actually obtained in this series of analyses: from 15.1 to 20.8‰, giving an annual range of 5.7‰.

During the Sangamon interglacial in central Illinois the climate was somewhat warmer than at present (Blackwell et al., in press). Average δ_{mw} in this area is approximately −6‰, which is about 3–4‰ heavier than meteoric waters in southern Ontario at present. *Castoroides* is substantially more massive than *Castor* so we expect that its isotopic response will be substantially less sensitive to variation in the $\delta^{18}O$ of its food or changing metabolic rate (Bryant and Froelich, 1995). Due to the greater size of *Castoroides* we also expect a steeper metabolic slope than in *Castor,* but if we assume the same metabolic slope (A) and offset (B) for the relationship between δ_w and δ_p as a working approximation, then we would expect that δ_{pe} values should be an average of 4‰ higher for the Hopwood sample. Average δ_{pe} for the latter is 18‰, which is about 6‰ higher than the average δ_{pe} of Ontario *Castor.* This suggests that the climate in the Sangamon was significantly warmer than today: perhaps more than 3°C warmer than now. Various other data confirm that the last interglacial was significantly warmer than the present one, for example the preservation of raised beach levels well above the Holocene maximum. The uncertainties in this climate estimation reflect the difficulty of determining δ_{bw} response in an extinct animal: did *Castoroides* δ_{bw} variation reflect change in δ_w better than *Castor* δ_{bw} because of the extinct beaver's greater size (Bryant and Froelich, 1995) or does *Castor* δ_{bw} show a more exaggerated seasonal response due to faster water turnover and a greater oxygen contribution from ^{18}O enriched foods in summer? The seasonal variation in *Castor* δ_{bw} is probably greater than annual variation in the $\delta^{18}O$ of larger water masses in the area, based on analyses of temperate region surface waters (e.g., Mook, 1970).

The amplitude of the seasonal variation in *Castoroides* is significantly larger than that for any of the specimens of *Castor* studied here, which may partly result from greater control of δ_{bw} by varying δ_w due to its greater mass (Bryant and Froelich, 1995), or from giant beavers having had a significantly different subsistence pattern from modern beaver. The latter suggestion is partly supported by the dentition of *Castoroides:* the incisors closely resemble groundhog incisors (*Marmota monax*) while the molars are very similar to those of the capybara (*Hydrochoerus sp.*), neither of which feeds extensively on woody material. It is improbable that the warmer Sangamonian climate could have been accompanied by a wider annual range of δ_{mw}.

10. CONCLUSIONS

The oxygen isotopic composition of *Castor* enamel is probably a good monitor of δ_w, although the δ_{mw} signal is attenuated, mainly by mixing with pre-existing water masses and a lag in the response of δ_{bw}. Because beaver are relatively restricted in the water that they sample, as well as consuming water freely, they are apparently sensitive to even small hydrological effects such as differences in amounts of runoff or evaporation at the end of summer and changes in the balance between lake and stream water. Beaver teeth record short-term variation not previously found elsewhere because of their rapid tooth growth, but a number of teeth must be analyzed to define a full annual cycle and to permit calculation of the δ_p/δ_{mw} relationship. The bone of adult beaver within the study area has a relatively constant value of 11.9 ± 0.5‰ and is suitable for the interpretation of mean annual temperatures. δ_{pb} can be approximated in fossil material from the range of δ_{pe}. The following can in many cases also be learned from beaver δ_{pe}:

1) Degree of seasonality (variation in δ_w over a year).
2) Relative rates of spring increase in δ_w vs. winter decrease.
3) The presence of a meltwater signal as a delayed pulse of low δ_w.
4) Season of death (for example the *Castoroides* studied probably died in the autumn or winter).
5) Major influences of lake water or ground water.
6) An approximation of the rate of tooth growth.

The teeth contain a reliable, self-checking, mechanism for detecting diagenesis as no teeth should have a similar δ_{pe} along their length. Bone or dentine δ_p can be checked for validity against the δ_{pe} data.

By combining results from *Castor* with less water dependent mammals, such as deer or marmots (*Marmota*), it may be possible to identify effects resulting from changes in relative humidity in periods when reliable hydrogen isotopic data are not available. An initial examination of the giant beaver (*Castoroides ohioensis*) indicates that its teeth preserve an excellent record of seasonal variability in δ_w and the relative temperatures of interglacial periods can be compared using them. If δ_w can be determined from *Castoroides,* then fish and aquatic reptile bones can be used to determine the temperature of the water.

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Appendix A. Sample identification and isotopic analyses. All isotopic analyses are quoted as permil VSMOW.

Sample		$\delta^{18}O$	Sample		$\delta^{18}O$	Sample		$\delta^{18}O$
EBA 1	2.01	10.8	GT 2	2.1	14.6	TL 3	3.1	13.8
	2.04	10.8		2.3	13.8		3.3	14.0
	2.07	10.6		2.5	13.4		3.5	13.5
	2.10	10.6	bone		12.5		3.7	12.6
	2.12	10.2					3.9	12.3
	2.14	10.5	GT 3	3.1	12.8	bone		12.4
	2.16	10.2		3.3	12.4			
bone		11.8		3.5	12.3	TL 4	4.1	14.3
				3.7	11.8		4.25	13.2
EBA 2	3.01	11.4		3.9	11.2		4.4	13.3
	3.02	11.2	bone		11.2		4.6	13.3
	3.03	11.1				bone		13.2
	3.05	11.2	GT 4	4.1	13.4			
	3.06	10.8		4.3	14.0	TL 5	5.1	13.8
	3.07	10.5		4.5	14.1		5.3	13.6
	3.08	10.8		4.7	13.8		5.5	13.1
	3.09	10.5		4.9	13.5		5.7	12.2
	3.10	10.6	bone		12.7	bone		12.2
	3.11	10.6						
	3.12	10.5	GT 14	14.2	13.9	TL 6	6.1	13.3
	3.13	9.6		14.5	14.5		6.3	14.2
	3.14	10.2		14.7	14.4		6.5	14.6
	3.15	10.0	bone		12.4		6.7	13.4
	3.16	9.8				bone		11.9
	3.17	10.1	TL 1	1.1	13.1			
bone		11.5		1.3	12.0	TL 7	7.1	14.0
				1.5	11.5		7.3	13.3
EB 2	2.1	13.0		1.7	10.9		7.5	13.1
	2.3	13.7	bone		10.7	bone		13.4
	2.5	13.5						
bone		11.9	TL 2	2.1	13.7	TL 8	8.1	13.9
				2.3	12.7		8.3	14.8
GT 1	1.1	15.0		2.5	12.6		8.5	14.1
	1.3	15.0		2.7	12.7		8.7	12.9
	1.5	14.4		2.9	12.3		8.9	12.5
bone		13.7	bone		11.3	bone		11.7

Notes on sample data: EBA = Erin (Ontario) adult beaver. EB = Erin (Ontario) juvenile beaver. GT = Georgetown (Ontario), TL = Beavers from Parry Sound area (Ontario) (trapper = Terry Little). The sample numbers consist of (Identifier. Measurement)—where the identifier is the beaver number from the area. The measurement is the distance in centimetres (approximately) from the base of the enamel for all the beavers apart from the 2 EBA beavers, where the samples are numbered every 5 millimeters from the tip of the incisor.

The analyses of *Castoroides* (from the sawn base of the tooth toward the tip) are:

Base 18.9, 19.1‰ (duplicates)
2 20.4‰
3 17.0‰
4 15.4‰
Tip 19.7‰
Dentine: 18.7‰.