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# Reflections of surface water, seasonality and climate in stable oxygen isotopes from tyrannosaurid tooth enamel

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## Abstract

Patterns of isotopic variation in enamel of eight *Albertosaurus* teeth from the Campanian/Maastrichtian Horseshoe Canyon Formation, Alberta, were measured by serial sampling along the growth axis. Cycles in the isotopic values appear to correlate to published tooth growth rates for tyrannosaurids. Tyrannosaurid dinosaur teeth of ~50 mm in length provide ideal repositories of terrestrial climatic information as each records a full annual cycle of body water isotopic variation. The relatively thin enamel precludes problems associated with time-averaging associated with complex growth patterns found in thick mammalian enamel. The most consistent and striking pattern associated with all of the teeth are two relatively closely spaced subequal maxima. These appear to be associated with onset of a seasonal episode of high humidity after the activation of the “amount effect,” where the influence of ambient temperature on surface water (and body water)  $\delta^{18}\text{O}$  ends while temperatures remain above 20 °C. Teeth within a single fossiliferous horizon show the same general isotopic pattern and range. A notable difference in pattern shape and magnitude of isotopic variation between tyrannosaurid teeth from several stratigraphic intervals of the lower Horseshoe Canyon Formation section indicates a climatic changes from strong seasonality (high annual temperature range with distinct precipitation and humidity maxima during each year) at the base of the section to milder seasonality at the top.

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**Keywords:** Isotope; Oxygen; Dinosaur; Enamel; Paleoclimate; Amount effect

## 1. Introduction

Biogenic phosphate minerals such as bone, dentine, and enamel are now regularly used as recorders of paleoenvironment (see Barrick, 1998 for review).

Biogenic phosphates derive their phosphate  $^{18}\text{O}/^{16}\text{O}$  signal ( $\delta^{18}\text{O}_p$ ) from the body water reservoir  $\delta^{18}\text{O}$ . Isotopically, this reservoir is a combination of three oxygen sources: ingested water (drinking water and water in food), food solids, and atmospheric oxygen (Fig. 1; Bryant and Froelich, 1995; Kohn, 1996; Barrick, 1998). Of the three inputs to the body water reservoir, drinking (meteoric) water dominates the reservoir isotopic ratio and varies with temperature (Luz and Kolodny, 1989; D’Angela and Longinelli,

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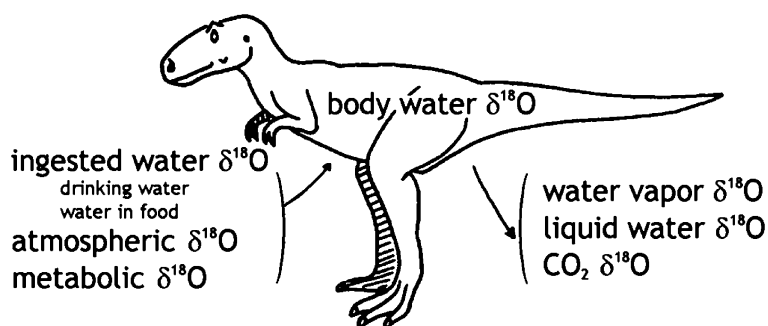


Fig. 1. Fluxes of oxygen contributing to isotopic ratio of body water reservoir in theropod dinosaur (modified from Bryant and Froelich, 1995).

1990) and evaporative enrichment (Kohn, 1996). Food and food water isotopic ratios are related to meteoric water but are also modified by changes in relative humidity through the evapotranspirative enrichment of leaves (Cormie et al., 1994). Deciphering an animal's  $\delta^{18}\text{O}_p$  signal is also complicated by the effect of the animal's thermoregulatory strategy. In most heterotherms,  $\delta^{18}\text{O}_p$  is also influenced by changes in body temperature (Barrick et al., 1992, 1993, 1996; Fricke and Rogers, 2000; but see Barrick et al., 1999) whereas in homeotherms bone forms at a constant temperature and preserves the variation in body water  $\delta^{18}\text{O}$  alone (D'Angela and Longinelli, 1990; Bryant et al., 1994; Barrick and Showers, 1995; Barrick et al., 1996). Therefore, phosphates of homeotherms are manufactured containing an oxygen isotope record related to surface water and humidity (Kohn, 1996).

Bone is often remodeled in vivo and susceptible to overprinting by the addition of secondary, external phosphate after burial, both processes which can disrupt the record of body water  $\delta^{18}\text{O}$ . Tooth enamel is more dense, more crystalline, and less organic than bone and is hence more resistant to post-depositional modification (Lucas and Prévôt, 1991). Early studies reported phosphate  $\delta^{18}\text{O}$  from tooth enamel of bears (Reinhard et al., 1996), elephants (Ayliffe et al., 1992, 1994), horses (Bryant et al., 1994, 1996; Sanchez-Chillon et al., 1994), and dinosaurs (Fricke and Rogers, 2000; Jensen, 2000; Jensen et al., 2000), using whole teeth to produce a single isotopic value, usually because the analytical technique required samples of up to 200 mg. Serial sampling of a single tooth, in which

samples are collected as a series of bands or spots paralleling growth lines from tooth root to crown (Hillson, 1986), has been employed for isotopic studies of carbon and oxygen in teeth (Lee-Thorp et al., 1997; Cerling et al., 1998; Hobson and Sease, 1998; Balasse et al., 2001) and has worked on thickly enameled or very large teeth of beaver (Stuart-Williams and Schwarcz, 1997), zebra, gazelle (Kohn et al., 1996, 1998), horse (Cerling and Sharp, 1996; Sharp and Cerling, 1998; Feranec and MacFadden, 2000), bison (Gadbury et al., 2000), sheep (Fricke and O'Neil, 1996), rhinos (Dettman et al., 2001), Miocene gomphotheres (Fox and Fisher, 2001), Paleocene pantodonts (Fricke et al., 1998), and in the tusks of elephants (Koch et al., 1989, 1998). Each of these studies revealed seasonal variation in enamel  $\delta^{18}\text{O}$  in tooth enamel phosphate and/or enamel carbonate. Until recently, however, the combination of enamel phosphate oxygen isotopic analysis with high-resolution isotopic sampling has been unavailable. New wet chemistry and preparation techniques, transformation of enamel to silver phosphate (Dettman et al., 2001), and pyrolysis mass spectrometry (Koziet, 1997; Showers et al., 2002), have substantially reduced the minimum sample size required for analysis of  $\delta^{18}\text{O}_p$ . High-resolution serial sampling may now be applied to small and/or thinly enameled teeth, such as those of theropod dinosaurs.

Here, enamel from eight teeth of the tyrannosaurid theropod *Albertosaurus* from latest Campanian Horseshoe Canyon Formation of south-central Alberta has been serially sampled and analyzed isotopically to search for a seasonality signal in

$\delta^{18}O_p$ . Results are compared to published estimates of tooth growth rate in theropod dinosaurs (Erickson, 1996a) and results compared to theoretical both within and between several stratigraphic intervals from the same succession.

## 2. Methods

### 2.1. Collection of dinosaur teeth

Eight nearly complete adult *Albertosaurus* teeth used in this study were collected during a stratigraphic and taphonomic survey in the lower Horseshoe Canyon Formation (Straight and Eberth, 2002; Fig. 2). The 210-m-thick succession of fossil-rich fluvial sediments of the lower Horseshoe Canyon Formation were deposited as a part of a clastic wedge on the Western Interior Seaway during the final 2 my of the Campanian (Catuneanu and Sweet, 1999). The succession includes nearly 15 m of coal, almost 80 m of carbonaceous mudrocks, and a fossil record of subtropical plants, including fossilized remains of palms, cypress, and ferns, indicating a wet, seasonally warm climate during the late Campanian. The coals and carbonaceous mudrocks are more abundant toward the base of the formation, and the stratigraphic data indicate a general decrease in surface wetness through the time recorded by the succession (Straight and Eberth, 2002).

Vertebrate fossils of the lower Horseshoe Canyon Formation are preserved in laterally continuous, chronostratigraphic fossiliferous horizons of one to four meters in thickness, separated by intervals of generally less fossiliferous strata (Straight and Eberth, 2002). Like most of the fossils in the lower Horseshoe Canyon Formation, the tyrannosaurid teeth used in this study came from floodplain mudrocks or siltstones, with no evidence of reworking, pre-burial weathering, of post-burial alteration. The stratigraphic position of fossils and the horizons containing them is described in terms of meters above formation base (m AFB; Fig. 2). The eight teeth analyzed here represent five important fossiliferous horizons in the lower Horseshoe Canyon Formation and were analyzed isotopically to assess  $\delta^{18}O_p$  variation in one taxon through time. Tooth H021 represents a sparse fossiliferous horizon at 17



Age	PM	m	Lithostratigraphy	coal & sands	surfaces & teeth
Maastrichtian Pal.	28n	300	EDMONTON GROUP	14	K-T Boundary (Nevis)
	29n			13	
	29r			12	
	30n			11	
	31n			10	
Campanian	32r	200	EDMONTON GROUP	9	G008 (170 m)
				8	D039 (150 m)
				7	D011 (145 m)
				6	B148 (129 m)
				5	(83-84.5 m)
				4	F010, F007b, F027
				3	
				2	
1	H021 (17 m)				
0					

Fig. 2. Location and stratigraphic relationships for theropod tooth collection sites in the Horseshoe Canyon Formation of Alberta, Canada. The PM column indicates the paleomagnetic record for the Edmonton Group (Eberth, 2002). The base of the Horseshoe Canyon Formation is the baseline for both thickness (m, in meters) and the numerical hierarchy for major coal seams (Gibson, 1977; Straight and Eberth, 2002); Coal Seam 13 within the Scollard Formation is also known as the Nevis Coal Seam and marks the Cretaceous–Paleocene (K–T) boundary. Intervals dominated by kilometer-wide sandstone units >10m thick are labeled as SS. Sequence boundaries (SB) indicate changes in facies and architecture of deposits; their positions are approximate.

m AFB in fluvial deposits reflecting a transition to fluvial control on deposition. Three teeth, F010, F007b, and F027, come from the most fossiliferous

horizon in the section between 83 and 84.5 m AFB. One tooth, B148, comes from a thin horizon at 129 m AFB. Two teeth, D039 and D011, come from two closely spaced fossiliferous horizons between 146 and 151 m AFB, respectively. The last tooth, G008, comes from fluvial strata at 170 m AFB in an interval informally termed the Drumheller Marine Tongue.

## 2.2. Growth and sampling of dinosaur teeth

Sediment was removed from the fossil teeth by a sonic bath, and fossil preparatory tools were used to remove additional museum preservative, adhesive, or resistant matrix from the enamel surface. Samples were collected using a carbide bit in a low-speed rotary drill. Each sample of 1–4 mg of powder was collected from a shallow groove in the enamel, usually down to the surface of the dentine, nearly parallel to lines of cross-section (Fig. 3).

The rationale for this sampling pattern comes in part from previous work involving serially sampled mammal teeth (Fricke and O'Neil, 1996) and in part from histological studies describing the growth of theropod teeth (Erickson, 1996a; Sander, 1999). Teeth of *Albertosaurus* are posteriorly curved cones

of dentine covered by a 150- $\mu\text{m}$ -thick sheath of enamel (Fig. 3; Sander, 1999), composed of 99% inorganic carbonate hydroxyapatite or dahllite (Hillson, 1986; Lucas and Prévôt, 1991; Rink and Schwarcz, 1995). Tooth growth commences at the tip with a cone of dentine extending rootward by the daily addition of a layer of dentine, in *Albertosaurus* averaging 15  $\mu\text{m}$  thick, inside the previous growth, forming the lines of von Ebner (Erickson, 1996a; Dean, 2000). Where the dentine cone extends the length of the tooth, enamel forms a circular band (incremental line or regular striation of Retzius) inclined toward the tooth tip from the enamel–dentine junction (Sander, 1999; Dean, 2000). Incremental lines in dentine (lines of von Ebner) and enamel (short-period lines, regular striae of Retzius) both represent daily growth and thus form in tandem, although individual lines may not be continuous from one material to the other (Fig. 3; Dean, 2000). The transverse bands of enamel are visible as thin color bands and/or as surface undulations in the enamel of tyrannosaur and other coeval theropod teeth among the survey specimens collected from the lower Horseshoe Canyon Formation (Fig. 4). Where such features were visible on the teeth used in this study, they were used as guides for sample grooves. Sampling trenches were kept narrow, about 1 mm in width, to minimize time-averaging through the inclusion of numerous incremental lines. In teeth with thicker enamel, the apical cant of incremental lines results in time-averaged samples even in serial analysis (Hoppe and Amundsen, 2001), but in tyrannosaurids the thin enamel and the subordination of incremental lines to parallel, columnar crystallites perpendicular to the enamel surface (Sander, 1999) minimize the degree of time-averaging with sampling depth.

Enamel powder was prepared for analysis following the method detailed in the data repository for Dettman et al. (2001). Samples were dissolved in 1 ml 2M HF to liberate the phosphate anion. Solids were removed, the remaining solution diluted to 10 ml, and then 0.8 ml of 20%  $\text{NH}_4\text{OH}$  (6% by assay) and 1 ml of 2M  $\text{AgNO}_3$  were added to instantly precipitate a cloud of brilliant yellow  $\text{Ag}_3\text{PO}_4$  particles. With centrifuging the  $\text{Ag}_3\text{PO}_4$  mud flocculates, and with drying turns into bright yellow powder. Phosphate yields for samples over 2.0 mg

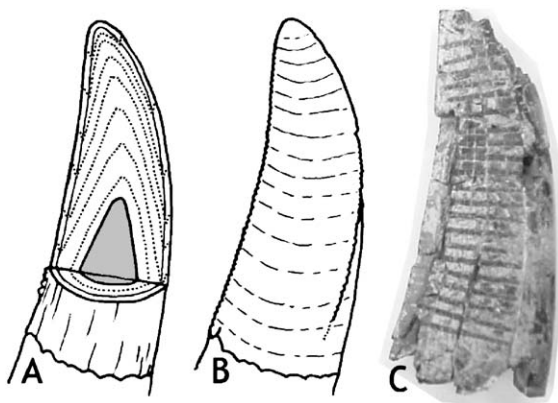


Fig. 3. Incremental growth bands and structure of a theropod tooth. (A) Cut-away section revealing incremental bands (lines of von Ebner) in dentine (cones expanding toward tooth root) and in the enamel sheath (striae of Retzius; enamel thickness exaggerated for clarity). (B) Incremental bands on enamel surface produce gently arcing growth lines transverse to tooth length. (C) Sampling pattern used on tooth RTMP1.

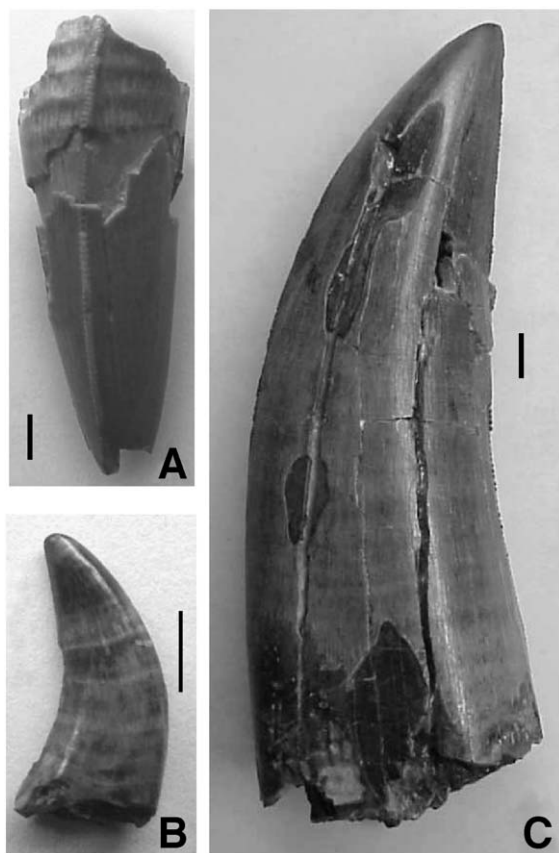


Fig. 4. Visual cues guiding sample collection in the surface texture (A) or color (B, C) on fossil theropod teeth. (A) *Albertosaurus* and (B) *Saurornitholestes*, both from lower Horseshoe Canyon Formation. (C) Tyrannosaurid tooth from Dinosaur Provincial Park. Scale bars are 5 mm.

were  $100 \pm 5\%$ , whereas phosphate recovery degrades for smaller enamel samples. This loss of phosphate occurs because as the smaller samples dry they adhere to the sides of the centrifuge tube rather than forming a pellet as in larger samples. This incomplete recovery does not correlate with  $\delta^{18}\text{O}_p$  in standards.

Silver phosphate samples averaging 0.5 mg were packed in  $3.5 \times 5$  mm silver capsules, then thermally decomposed at  $1450^\circ\text{C}$  in an automated Finnigan MAT Delta Plus TCEA (at either North Carolina State University or the University of Arkansas Stable Isotope Lab) connected to a continuous-flow GC mass spectrometer under an anoxic atmo-

sphere (Showers et al., 2002). Results were compared to a CO reference gas to get a raw  $\delta^{18}\text{O}_p$  value and corrected against two or three reference standards, including NBS 120c (Florida Phosphate Rock, 21.6‰), NBS 8542 (sucrose, 36.3‰), and NBS 127 ( $\text{BaSO}_4$ , 9.1‰). Isotopic data are reported in standard delta notation (Table 1 and Appendix), based on the relation between each sample and standard mean ocean water (V-SMOW),

$$\delta^{18}\text{O} = \left[ \frac{(^{18}\text{O}/^{16}\text{O})_{\text{sample}}}{(^{18}\text{O}/^{16}\text{O})_{\text{standard}}} \right] - 1 \times 10^4. \quad (1)$$

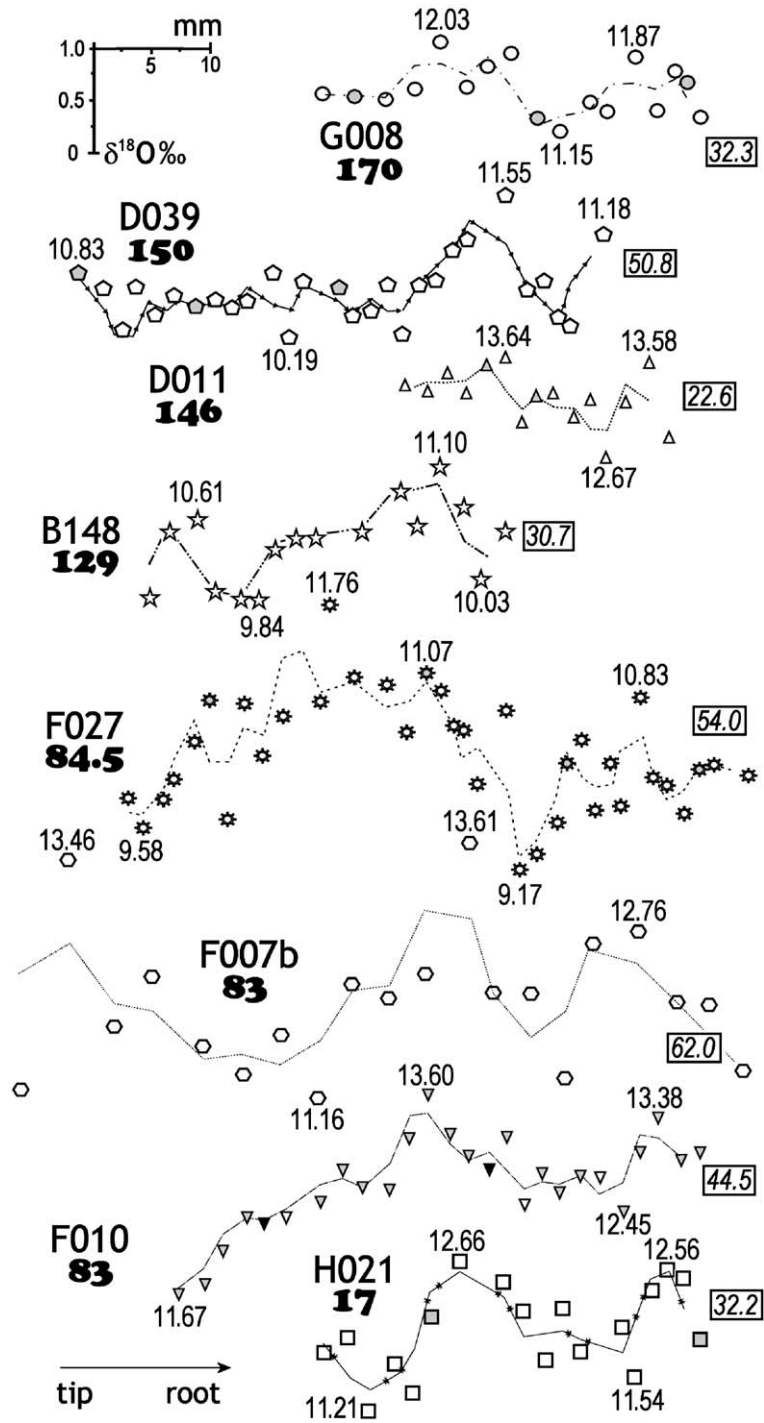
### 2.3. Diagenesis

Stable isotope geochemistry on biological apatite as a paleoenvironmental recorder has been repeatedly challenged on the grounds that the process of fossilization results in diagenetic alteration. Recent theoretical studies conclude that stable isotopic records in biogenic phosphate are typically diagenetically destroyed (Sanchez-Chillon et al., 1994; Hubert et al., 1996) or altered either by partial dissolution of phosphate during recrystallization of apatite crystals (Iacumin et al., 1996a), by microbial reprecipitation (Ayliffe et al., 1994; Kolodny et al., 1996; Blake et al., 1997), or through interaction with groundwater and/or other sources of phosphate (Wang and Cerling, 1994; Iacumin et al., 1996b).

Table 1  
Stratigraphic position and isotopic summary for tyrannosaurid teeth used in this study

	Elevation (m AFB)	Length (mm)	Max $\delta^{18}\text{O}$ (‰)	$\delta^{18}\text{O}$ range (‰)
H021	17	32	12.66	1.45
F010	83	45	13.60	1.93
F027	83	54	11.76	2.60
F007b	84.5	62	13.61	2.45
B148	126	30	11.10	1.26
D011	146	23	13.64	0.97
D039	150	45	11.55	1.36
G008	170	32	12.03	0.87

Elevation lists each tooth's stratigraphic level above the basal contact of the Horseshoe Canyon Formation in meters.



However, diagenetic disruption of isotopic signals in continental vertebrate fossils is probably infrequent. The model of fossils as francolite pseudomorphs of bone (Hubert et al., 1996; Kolodny et al., 1996) is derived from a study of the process of phosphatization of marine carbonate deposits to form phosphorites (Shemesh et al., 1988; Jarvis, 1992; Blake et al., 1997). In the marine environment, microbes deposit phosphate minerals derived from  $\text{PO}_4$  in organic material buried within a carbonate mineral matrix (Jarvis, 1992). The minor amount of skeletal phosphate present is overprinted by diagenetic phosphatic cements, which preserve isotopic characteristics of the depositional environment. By contrast, fossil bone and teeth in most fluvial rocks are preserved as hydroxyapatite or carbonate hydroxyapatite instead of francolite, due to the relative immobility and rarity of both fluorine and phosphate in fluvial sediments (Pate et al., 1989; Lucas and Prévôt, 1991; Person et al., 1995; Barker et al., 1997). X-ray diffraction and histological studies of bone, enamel, and dentine from fossils from lower Horseshoe Canyon Formation fossil surveys, including teeth used in this study, show uniform preservation as carbonate hydroxyapatite (Straight and Eberth, 2002). Microbial modification of bone is rare in terrestrial soils, where most organic constituents in bone are lost to photolysis during weathering (Koch et al., 2000) and most alteration involves addition of trace elements rather than removal of phosphate (Bocherens et al., 1994; Kohn et al., 1999). In cases where microbial reprecipitation of bone mineral does occur, the reduction of organic material does not disrupt the  $\text{PO}_4$  anion in preexisting phosphate minerals (Jarvis, 1992), wherein the paleoecological  $\delta^{18}\text{O}$  signal is preserved. Such reprecipitation produces a distinctive, easily detectable morphology in fossil bone (Koch et al., 2000; Nielsen-Marsh and Hedges, 2000) and produces diagenetic phosphate cement proportional to the

mass of organic material from which it was derived, relatively small compared to the mass of bone phosphates. The low organic mass and low porosity of tooth enamel and the relatively large size of microbes capable of metabolizing skeletal phosphate indicate that microbially mediated diagenetic phosphate within tooth enamel is highly unlikely (Kohn et al., 1999).

Diagenetic homogenization that nevertheless maintains histological characters (Hubert et al., 1996) is frequently invoked to explain isotopic variation seen in skeletal phosphate  $\delta^{18}\text{O}_p$  (Ayliffe et al., 1992, 1994; Sanchez-Chillon et al., 1994; Iacumin et al., 1996a,b); a more parsimonious interpretation is that variation arises from intricately recorded biological signals (interbone and intrabone variation sensu Barrick and Showers, 1994, 1995; Barrick et al., 1996; and intra-tooth variability in Hobson and Sease, 1998; Kohn et al., 1998; Feranec and MacFadden, 2000; Dettman et al., 2001; this study) undetected by past analytical and sampling techniques.

### 3. Results

Results for enamel  $\delta^{18}\text{O}_p$  are tabulated (Table 1; Appendix A) and graphically displayed (Fig. 5) with the vertical axis serving as both an isotopic variation axis and for relative stratigraphic position; the horizontal axis shows distance from tooth tip to reflect the passage of time and tooth growth. All patterns feature two subequal maxima; longer patterns feature two unequal minima. G008, D039, D011, and B148 feature low-amplitude variation, whereas F010, F027, F007b, and H021 feature a high-amplitude  $\delta^{18}\text{O}_p$  signal. The graph for each tooth (Fig. 5) also features a two-point running average line to smooth out analytical error, to clearly separate the isotopic profiles, and to display isotopic trends within each pattern.

Fig. 5. Enamel oxygen isotope data from eight serially sampled tyrannosaurid teeth. Patterns distributed to avoid overlap; horizontal and vertical scale consistent within but not between individual tooth patterns. Small numbers display boundary isotopic values in per mil, boxed numbers display distance of last sample from tooth tip in millimeters. Gray points indicate two averaged measurements of the same sample, black points indicate three. Large bold values under sample names indicate elevation above the base of the Horseshoe Canyon Formation. Lines are two-point running averages of data to clearly separate profiles while displaying similarities among isotopic trends between patterns.

## 4. Discussion

### 4.1. Growth rate

Recovery of a complete twin-peaked annual  $\delta^{18}\text{O}_p$  cycle from a tyrannosaurid tooth requires a tooth crown with a  $\sim 55$  mm long sheath of enamel. Slightly more than half of full tooth length is root in tyrannosaurids, hence the isotopic results imply that a 11 cm tooth with root represents two years of growth. This result contrasts with estimates from Johnston (1979) an eight-year growth period for tyrannosaurid teeth, but his interpretation has been criticized. The more recent work of Erickson (1996a,b) found virtually identical daily incremental growth lines in dentine of mammalian, dinosaur, and crocodylian teeth. The addition of a daily incremental line with a mean thickness of  $15\ \mu\text{m}$  to a growing tyrannosaurid tooth (Erickson, 1996a) results in between 51 and 62 mm growth/year for tyrannosaurids, and between 51 and 53 mm/year for *Albertosaurus*. Erickson's (1996a) estimate of 519 days for growth of an average tooth in an adult *Albertosaurus* indicates that average complete tooth (crown+root) should be 78 mm long, with a corresponding crown length of  $\sim 39$  mm. Fourteen complete *Albertosaurus* crowns (tooth sans root) recovered from the survey in the lower Horseshoe Canyon Formation (Straight and Eberth, 2002) feature an average crown length of 36 mm. *Albertosaurus* tooth size and oxygen isotopes from this study are consistent with growth rate estimates from Erickson (1996a). Tooth length of smaller dinosaurs precludes seasonal climate analysis as only a very short part of an annual cycle is recorded. Similar problems occur when analyzing highly worn teeth.

### 4.2. Correlation with body water models

Longinelli and Nuti (1973) first empirically derived an equation correlating the isotopic oxygen values from biogenic phosphates in invertebrates to environmental temperatures and water oxygen isotope values,

$$T\ (^{\circ}\text{C}) = 111.4 - 4.3(\delta^{18}\text{O}_p - \delta^{18}\text{O}_w). \quad (2)$$

Kolodny et al. (1983) empirically confirmed the correlation between temperature and phosphate  $\delta^{18}\text{O}_p$  values, demonstrating that fish body water and environmental water  $\delta^{18}\text{O}$  values are in equilibrium. Luz and Kolodny (1985, 1989) validated the equation for mammals, showing that bone  $\delta^{18}\text{O}_p$  values are in equilibrium with body temperature and body water  $\delta^{18}\text{O}$  values rather than with environmental temperatures and meteoric water  $\delta^{18}\text{O}$  values. Many studies have found variable relationships between body water and meteoric water  $\delta^{18}\text{O}$  values depending upon diet, humidity, and physiology (e.g., Longinelli, 1984; Luz et al., 1984; D'Angela and Longinelli, 1990; Bryant et al., 1996; Kohn, 1996).

Kohn (1996) created a comprehensive model for predicting the effects of diet and physiological adaptation on body water and bone  $\delta^{18}\text{O}$  values. For carnivores, the predicted relationship between bone or enamel  $\delta^{18}\text{O}_p$  and surface water  $\delta^{18}\text{O}$  values is:

$$\delta^{18}\text{O}_p = 21.3 - 3.0h + 0.74(\delta^{18}\text{O}_{\text{sw}}), \quad (3)$$

where  $h$  is relative humidity. The correlation between surface water  $\delta^{18}\text{O}$  and body water  $\delta^{18}\text{O}$  values for carnivores at 75% relative humidity is:

$$\delta^{18}\text{O}_{\text{bw}} = 0.74(\delta^{18}\text{O}_{\text{sw}}) + 1.47. \quad (4)$$

Prior to interpreting the isotopic patterns in tyrannosaurid teeth with respect to climatic factors, the general relationship for carnivores and surface water  $\delta^{18}\text{O}$  in Eqs. (3) and (4) must be demonstrated valid for carnivorous dinosaurs. Applying a typical range of relative humidity values (30–80%) and the range of measured  $\delta^{18}\text{O}_p$  values from the tyrannosaur teeth to Eq. (3), surface water  $\delta^{18}\text{O}$  derived from enamel in this study fall between  $-7.2\text{‰}$  and  $-15.5\text{‰}$ , usually below  $-12\text{‰}$ . These results are consistent with an independent determination of surface water  $\delta^{18}\text{O}$  from this region of Alberta from Campanian turtle bone phosphate, showing a range from  $-9.5\text{‰}$  to  $-11.5\text{‰}$  (Barrick et al., 1999).



#### 4.3. Influences of ecology and physiology on isotopic pattern

In homeothermic carnivores such as tyrannosaurids (Barrick and Showers, 1994), isotopic changes in body water are a reflection of changes in local surface water for two reasons. First, the body water  $\delta^{18}\text{O}$  of homeotherms is not influenced by environmental temperature. Second, the carnivore's body water reservoir includes both drinking water consumed by the carnivore and drinking water from the body water of prey (Kohn, 1996). No trophic level effect has been demonstrated in  $\delta^{18}\text{O}$  of body water for predators' assimilation of prey (i.e., no fractionation has been shown between food water and body water  $\delta^{18}\text{O}$  values in predators). Most predators manufacture their body water primarily through drinking, whereas prey herbivores gain a large proportion of body water from foliage (Kohn, 1996). The  $\delta^{18}\text{O}_p$  of homeothermic predators should therefore provide a better record of surface water  $\delta^{18}\text{O}$  than that of herbivorous and/or heterothermic animals.

Sharp and Cerling (1998) found a relationship between body mass in some modern mammal species and enamel  $\delta^{18}\text{O}_p$ , in which the annual record of  $\delta^{18}\text{O}_p$  from enamel is attenuated relative to that for coeval surface water  $\delta^{18}\text{O}$  cycle. This signal dampening, as well as a delay in isotopic extremes, results from the long retention time of body water in very large animals (Nagy and Peterson, 1988). Precise effects of body mass on isotopic value, attenuation, and delay for dinosaurs, including the 3000 kg *Albertosaurus* used in this study, are not known. In this study, however, all teeth come from animals of at least subadult size, i.e., animals that had lived long enough to manufacture, wear out, and shed at least one set of teeth, probably >2 years (Erickson, 1996a). Hence the effect of body mass on enamel  $\delta^{18}\text{O}_p$ , if any, for these eight teeth should be approximately consistent.

#### 4.4. Influences of climate on isotopic pattern

Surface water  $\delta^{18}\text{O}$  is critical to several models designed to reconstruct mean annual or mean monthly temperature. Enamel  $\delta^{18}\text{O}_p$  values from several types of mammals have been used to approximate

paleotemperature by first transforming  $\delta^{18}\text{O}_p$  into surface water  $\delta^{18}\text{O}$  through metabolic relationships (Bryant and Froelich, 1995; Kohn, 1996) and then transform it again using a relationship between surface water  $\delta^{18}\text{O}$  and temperature (Dansgaard, 1964; Gat, 1980; Rozanski et al., 1993; Fricke and O'Neil, 1999),

$$\delta^{18}\text{O} = 0.69T - 13.6. \quad (5)$$

Temperature and humidity vary on a regional scale due to elevation, latitude, and proximity to shorelines. Both influence surface water  $\delta^{18}\text{O}$ , with high temperature and low humidity each promoting enriched  $\delta^{18}\text{O}$  values, with temperature the stronger of the two controls. However, above a threshold temperature, further increases in temperature do not impact meteoric water  $\delta^{18}\text{O}$  due to the *amount effect*, defined as a relative depletion of precipitation  $\delta^{18}\text{O}$  values by  $\sim 1.5\%$  per 100 mm of precipitation (Dansgaard, 1964; Rozanski et al., 1993; Fricke and O'Neil, 1999). Typically, falling rain is progressively enriched by evaporation as it falls, but in air above a threshold temperature, enrichment of rainfall by evaporation ceases as the air through which the rainfalls becomes saturated. Eq. (5) implies that for an air temperature of 30 °C, surface water should be +6‰, but such precipitation values are never found (Rozanski et al., 1993; Fricke and O'Neil, 1999; Bowen and Wilkinson, 2002). Instead, based on the most positive precipitation values measured empirically from sites around the world, Eq. (5) is truncated above approximately 20 °C (Rozanski et al., 1993; Bowen and Wilkinson, 2002), at and above which precipitation does not exceed 0‰, even at locations with extreme warmth for some or all of the year. This depletion and the absence of precipitation  $\delta^{18}\text{O}$  values in excess of 0‰ are consequences of the amount effect. Kohn (1996) shows that surface water  $\delta^{18}\text{O}$  at both New Delhi and Rio de Janeiro never exceeds 0‰ in spite of temperatures in excess of 20 °C for at least 9 months out of the year. During New Delhi's summer when mean monthly temperatures remain over 30 °C, surface water  $\delta^{18}\text{O}$  drops from 0‰ to -6‰. Given that atmospheric saturation could occur with less evaporation under lower tempera-

ture, the threshold temperature for the engagement of the amount effect may be less than 20 °C at high altitude, at high latitude, or during winter months.

Above the threshold temperature, humidity becomes the critical control on precipitation  $\delta^{18}\text{O}$ . Precipitation falling into nearly saturated air rapidly engages the amount effect and thus retains its original, relatively depleted  $\delta^{18}\text{O}$  value of the precipitation as it leaves the cloud. Consequently, locations for which summer corresponds to the annual humidity maximum may have their lowest  $\delta^{18}\text{O}$  values during the hottest months. At Rio de Janeiro, where relative humidity is 80% all year, the annual signal is completely reversed relative to the predictions of Eq. (5), with southern-hemisphere summer months of January to March having the lowest surface water  $\delta^{18}\text{O}$  (Kohn, 1996). By contrast, highly arid regions such as the eastern Sahara feature the most positive  $\delta^{18}\text{O}$  values for precipitation, nearly 0‰ (Bowen and Wilkinson, 2002), because the dry air cannot

become saturated by the amount of precipitation falling through it. Due to the amount effect in climates regularly exceeding 20 °C, neither surface water  $\delta^{18}\text{O}$  nor enamel  $\delta^{18}\text{O}_p$  proxies can be converted reliably to temperature.

However, as surface water responds to climatologic controls, and given that carnivore enamel  $\delta^{18}\text{O}$  tracks surface water  $\delta^{18}\text{O}$ , comparisons of isotopic patterns from carnivore teeth should still reveal relative changes in the seasonal climate regime over several time scales. For comparative purposes, Fig. 6 shows eight hypothetical plots of mean monthly surface water  $\delta^{18}\text{O}$  for combinations of seasonality (high and low amplitude changes) and mean annual temperature (0, 3, 6, and 9 months with mean monthly temperature above the amount effect threshold). For both types of seasonality, the annual  $\delta^{18}\text{O}$  pattern shows two subequal maxima, reflecting the start and stop of amount effect influence, and a minimum between them associated with peak humidity. With relatively higher mean annual temper-

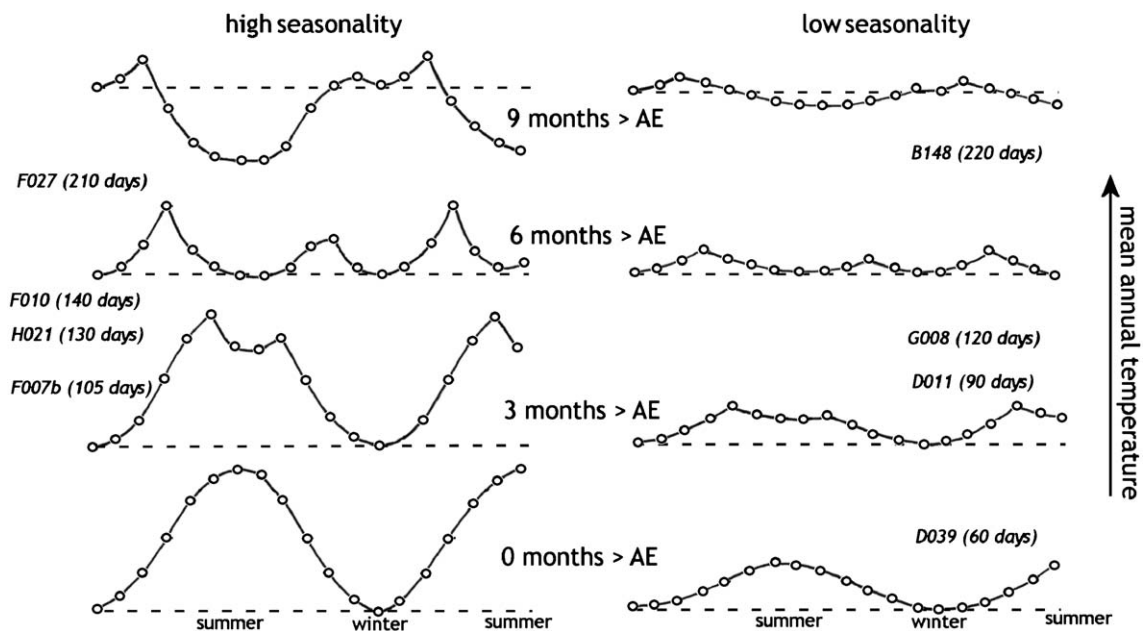


Fig. 6. Hypothetical variations of surface water  $\delta^{18}\text{O}$  over eighteen months for high- and low-seasonality environments. Vertical variation reflects the difference given the length of time (center, in months) during which temperatures exceed the amount effect threshold (AE). Results from tyrannosaur teeth are compared to hypothetical patterns and placed by matching signal amplitude and spacing between maxima (in parentheses, converted from millimeters to days given growth rate estimates).

ature, the amount effect is engaged for more months of the year (vertical axis, Fig. 6). Fig. 6 suggests that at locations when mean temperature always exceeds the amount effect threshold, isotopic patterns will be the reverse of those predicted by Eq. (5), consistent with Kohn's (1996) data from Rio de Janeiro.

#### 4.5. Pattern interpretation

The tyrannosaurid tooth enamel  $\delta^{18}\text{O}_p$  data compare closely to hypothetical surface water curves of Fig. 6. In each pattern, two maxima are interpreted as the timing for the engagement and cessation of the influence of the amount effect. The intervening minimum is interpreted as the point of maximum annual humidity and strongest influence over surface water and tooth enamel  $\delta^{18}\text{O}$  by the amount effect. The bimodal annual isotopic maximum has been detected in teeth of gazelles (Kohn et al., 1998) and possibly explains the bifurcated maxima and dissimilar minima of a  $\delta^{18}\text{O}_p$  seasonality record extracted from an elephant tusk (Koch et al., 1998). Narrowing of incremental lines associated with each minima in the tusk suggests reduced growth rate due to thermal stress (Koch et al., 1998); under this interpretation, the animal suffers thermal stress during summer heat as well as during winter cold.

The patterns from the tyrannosaurids in the survey can be divided into two groups based on amplitude, with H021, F007b, F027, and F010 showing high ( $>1.4\%$ ) amplitudes and B148, G008, D011, and D039 showing relatively lower amplitudes ( $<1.4\%$ ). If the spacing between the maxima on a cyclic pattern represents the period of the year during which the amount effect is generally engaged (i.e., the period of the year during which the average temperature exceeds  $20^\circ\text{C}$ ), each tooth can be compared to a specific hypothetical surface water trend in Fig. 6 by converting the spacing between the isotopic maxima from millimeters of enamel to days, using established growth rates for tyrannosaurids. For example, the separation of the two maxima for F010 is 20 mm, which given expected growth rates correlates to 130 days of amount effect influence during the year (Fig. 6); the same period for low-amplitude tooth D011

corresponds to 80 days. Applying this conversion to the eight teeth patterns, teeth below 130 m AFB (H021, F007b, F010, F027, and B148) reflect 4–7 months/year above the amount effect threshold, whereas teeth above 130 m AFB (D011, D039, and G008) reflect 2–4 months above the amount effect threshold (Fig. 6).

Isotopic results from tyrannosaurid enamel can be compared between teeth from the same fossiliferous horizon. Three teeth (F027, F007b, and F010) come from a fossiliferous horizon between 83 and 84.5 m AFB. All three teeth have high-amplitude cyclic signals and the highest isotopic ranges from the lower Horseshoe Canyon Formation, indicating a period of high seasonality (high annual temperature range with episodic precipitation and/or high humidity during only part of the year). By contrast, two teeth (D039, D011) from a fossiliferous horizon between 146 and 150 m AFB just below the transition to the Drumheller Marine Tongue feature low-amplitude cyclic signals interpreted as recording low seasonality (mild annual temperature and humidity range with relatively evenly distributed precipitation events through the year), with amplitudes of  $1.36\%$  and  $0.97\%$ , respectively, although the isotopic range of D011 may be underestimated due to its size.

Isotopic results from tyrannosaurid teeth can also be compared stratigraphically and correlated with changes in stratigraphic architecture, sedimentology, and paleoenvironment. Independent stratigraphic sections and sedimentological analyses indicate that a significant change in depositional setting occurs above Coal Seam 9 (Straight and Eberth, 2002; Eberth, 2002; "SB" in Fig. 2). Above this boundary, coal and organic mudrocks are less common, rooted horizons are more common, and all facies are generally thinner than similar examples below the boundary. Preserved channels and levees are thinner, narrower, and finer-grained above the boundary than below. Organic-rich mudrocks interpreted as wetland facies are significantly less common above the boundary, and clay-rich paleosol facies are more common. The stratigraphic data indicate a transition from a wet climate, in which the amount effect likely played a role in surface water  $\delta^{18}\text{O}$  values, to a drier climate, in which the amount effect would have been less important or inactive. Isotopic evi-

dence from the tyrannosaurid teeth in this study is consistent with these changes; teeth from below the boundary all exhibit high-amplitude isotopic patterns interpreted as reflecting high seasonality, whereas those from above the transition all exhibit low-amplitude isotopic patterns consistent with mild seasonality.

Considered in terms of maximum value (Table 1; Fig. 7), the teeth fall into two groups: H021, F010, F007b, and D011 all have maxima at or above 12.6‰, whereas F027, B148, D039, and G008 have maxima at or less than 12.0‰. Overlap between the two groups depends upon a single measurement, probably an outlier, in the F027 pattern (Fig. 7). In each group, mean  $\delta^{18}\text{O}_p$  trends upsection toward more positive values. The trends of both groups follow a similar slope and are separated by  $\sim 2.5$ ‰. One explanation for this non-stratigraphic grouping is that the data set contains teeth from two

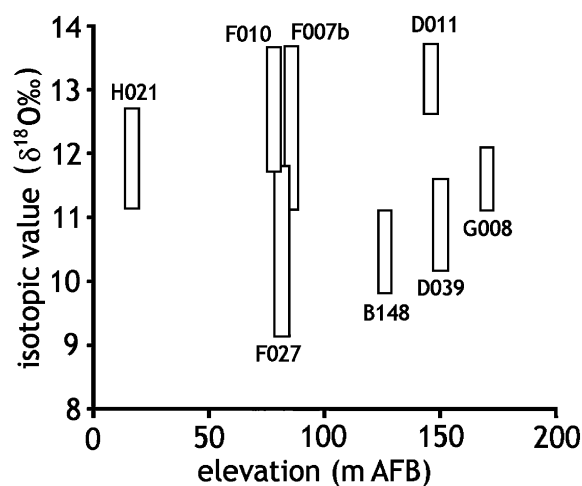


Fig. 7. Isotopic range versus elevation for the eight tyrannosaurid teeth. Elevation ( $x$ -axis) is recorded as meters above formation base (AFB). Teeth fall into two non-stratigraphic groups, separated by  $\sim 2.5$ ‰ and both trending upsection toward more positive mean  $\delta^{18}\text{O}_p$ . The overlap between F010, F007b, and F027 (slightly exploded along the  $x$ -axis for clarity) represents the only point of contact between the two groups and depends on one possibly anomalous point on the F027 pattern. These groups could reflect two distinct species of tyrannosaurids and/or some form of ecological separation (niche partitioning, migration, difference in diet, etc.).

types of tyrannosaur, consistent with faunal lists which indicate that up to four types of tyrannosaurs occur in the lower Horseshoe Canyon Formation, including *Aublysodon*, two forms of *Albertosaurus*, and *Daspletosaurus* (Braman and Eberth, 1988; Braman et al., 1995; Eberth et al., 2001). No unequivocal means yet exists to distinguish between individual species of tyrannosaur by dental morphology (Farlow et al., 1991; Baszio, 1997), as both the animals and the teeth they produce strongly overlap in size and design. A second explanation is that some of the tyrannosaurs fossilized in the lower Horseshoe Canyon Formation drink in one of two different regimes of mean annual temperature. If so, the groups could represent local niche partitioning (e.g., two water sources, such as non-local river water versus local, evaporatively enriched ponded water) or migratory behavior in one or both groups of animals. The parallel trends of isotopic enrichment are consistent with both groups experiencing equivalent climate change, probably related to an increase in mean annual temperature.

#### 4.6. Sampling technique

Previous studies incorporated several sources of isotopic variability and error inherent in techniques in which isotopic analysis of enamel resulted in one  $\delta^{18}\text{O}_p$  value for each tooth (Bryant et al., 1994; Iacumin et al., 1996a; Reinhard et al., 1996; Fricke and Rogers, 2000; Jensen et al., 2000). Measurement of  $\delta^{18}\text{O}_p$  from enamel homogenized by stripping a whole tooth does not adequately represent an annual mean unless the preserved growth period is exactly a year. Otherwise, the result will be biased toward the isotopic value of the last season of enamel growth (Fig. 8). Thus, single-value analyses of a collection of unrelated teeth will result in a range of values. A single enamel  $\delta^{18}\text{O}_p$  measurement from stripped tooth enamel formed in 9 months may vary from the actual annual mean by  $\pm 14\%$  of the annual seasonal isotopic range (Fig. 8). For example, in a tooth influenced by a 2‰ seasonal cycle, a whole-tooth measurement of enamel  $\delta^{18}\text{O}_p$  will vary by 0.57‰. From enamel formed over 6 months, the variation increases to  $\pm 30\%$ , and from enamel grown over 3 months,  $\pm 43\%$ . Enamel grown in periods of over a year can

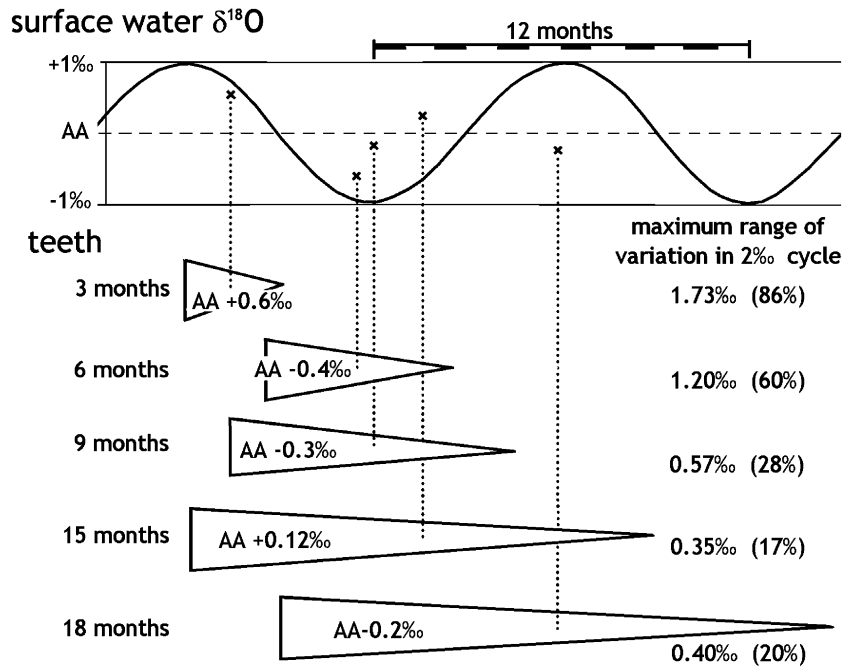


Fig. 8. Effects of single-measurement techniques on tooth enamel isotopic results. A hypothetical simple seasonal variation of surface water oxygen isotopes varies cyclically by 2‰ over a year. Sample teeth, positioned under the portion of the seasonal curve their enamel integrates and to right of their growth period in months, show effects of time-averaging on isotopic results. The value inside each tooth indicates the divergence from annual average (AA) for a single isotopic measurement of enamel; the cross above the midpoint of each tooth shows the measurement relative to surface water curve. Values to the right of each tooth indicate the maximum isotopic range, out of the 2‰ annual range and as a percentage of the annual range, between teeth formed over a period of months listed to the left of each tooth. Conical or tapering teeth and/or a more complex seasonality curve will result in more complex isotopic variability in teeth.

produce  $\delta^{18}\text{O}_p$  variation of  $\pm 10\%$  of the annual range (Fig. 8).

Stripping enamel from several teeth from different individuals of one species will not necessarily reveal the annual isotopic mean, particularly in mammals in which teeth are formed at a specific time during the animal's life. Mineralization of permanent molar (M1) among equids begins just before a late-spring birth and lasts 8 months (Nowak, 1991; Bryant et al., 1996). Consequently, most equid M1 teeth record the relatively enriched body water isotopic ratios experienced between early spring and mid winter. Therefore, a single-value measurement for each M1 in a population will generally overestimate the actual annual mean. This problem is further compounded by tooth wear, particularly in herbivores, destroying the oldest enamel, truncating the preserved isotopic record,

and commensurately increasing the potential range of isotopic variability. Theropod teeth are shed before developing significant wear and are continuously replaced, and consequently are less affected by these problems. However, conic or tapering teeth from theropod dinosaurs and canines from mammalian predators possess more enamel near the root than near the tip, biasing measurement of  $\delta^{18}\text{O}_p$  in a homogenized sample toward the last enamel formed.

Serial sampling avoids these sources of variability by reducing the time-averaging of the preserved isotopic record. The serial sampling technique therefore presents several new opportunities for isotopic treatment of fossil remains, including the stratigraphic applications employed in this study. Serial sampling provides a new test for diagenesis, as a cyclic signal in  $\delta^{18}\text{O}_p$  is unlikely to have been

caused by or survived diagenetic alteration. In animals in which several teeth are formed at the same time or continuously replaced, enamel isotopic records should preserve an overlapping, self-checking isotopic record of body water  $\delta^{18}\text{O}$ . The enamel record in teeth from dental batteries of dinosaurs (Patchus et al., 2001) or the tusks of elephants (Ayliffe et al., 1992, 1994; Koch et al., 1998) may allow a multi-year record of meteoric water changes to be assembled. Cross-sections of large dinosaur bones bear lines of arrested growth (LAGs; Sander, 2000; Curry, 1999), which if serially sampled may yield a multi-year proxy for meteoric water and humidity.

## 5. Summary

Seasonal variations in the body water  $\delta^{18}\text{O}$  of the theropod dinosaur *Albertosaurus* can be reconstructed by serially sampling enamel from unaltered teeth. The sampling technique used here avoids error associated with time-averaging associated with single whole tooth analyses or thick enamel. The continuous replacement and the thin enamel of dinosaur teeth make them ideal for retrieving high-resolution seasonal isotopic data. The patterns of these isotopic records are consistent with previously published tooth growth rates for *Albertosaurus*. Two general patterns arise from the isotopic data, consistent with evidence of changing climate regimes in the stratigraphic section of the lower Horseshoe Canyon Formation. The patterns are differentiated by the magnitude of the isotopic variation across the tooth and the shape of a double peak that likely arises from a seasonal jump in humidity. In addition, the eight teeth analyzed herein fall into two non-stratigraphic groups possibly associated with a taxonomic and/or ecological difference. Although the isotopic patterns in the enamel reflect variations in surface drinking water, these values cannot be accurately transformed into

mean monthly or seasonal temperatures as the relationship between temperature and meteoric water isotope values is invalid above approximately 20 °C at which point humidity has the strongest effect upon meteoric isotope values. However, the interaction between temperature and humidity do generate predictable patterns in the seasonal variations of meteoric isotope values. Recognition of these patterns in the stratigraphic record can lead to an understanding of shifts in general climate regime. These climate patterns may then be correlated to patterns of sediment accumulation or faunal/floral turnover within the stratigraphic record.

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## Appendix A

Enamel phosphate  $\delta^{18}\text{O}$  data from eight tyrannosaurid teeth from the lower Horseshoe Canyon Formation. Asterisks indicate that the isotopic values is an average of two (\*) or three (\*\*) replicate analyses.

H021		F010		F027		F007b		B148		D011		D039		G008	
Elevation	17 m	Elevation	83 m	Elevation	83 m	Elevation	84.5 m	Elevation	129 m	Elevation	146 m	Elevation	150 m	Elevation	170 m
mm	$\delta^{18}\text{O}$	mm	$\delta^{18}\text{O}$	mm	$\delta^{18}\text{O}$	mm	$\delta^{18}\text{O}$	mm	$\delta^{18}\text{O}$	mm	$\delta^{18}\text{O}$	mm	$\delta^{18}\text{O}$	mm	$\delta^{18}\text{O}$
from	(‰)	from	(‰)	from	(‰)	from	(‰)	from	(‰)	from	(‰)	from	(‰)	from	(‰)
tip	tip	tip	tip	tip	tip	tip	tip	tip	tip	tip	tip	tip	tip	tip	tip
32.2*	11.91	44.5*	13.03	54.0	10.04	62.0	11.49	30.2	10.48	22.6	12.86	44.8	11.18	32.3	11.29
30.7	12.50	42.9*	12.97	50.1	10.19	58.9	12.05	28.1	10.03	20.9	13.58	42.0	10.29	31.2*	11.63
29.4	12.58	41.0*	13.38	48.8*	10.13	56.2	12.08	26.6	10.71	18.9	13.21	41.0	10.38	30.1	11.74
28.0	12.39	39.4*	13.04	47.4	9.70	52.9	12.76	24.6	11.10	17.2	12.67	39.8	10.72	28.5	11.35
26.5	11.54	38.0*	12.45	46.0	9.97	49.1	12.64	22.7	10.54	15.8	13.23	38.3	10.64	26.7	11.87
25.4	12.03	36.0	12.80	44.8	10.06	46.6	11.35	21.3	10.88	14.4	13.06	36.5	11.55	24.3	11.35
21.9	11.79	34.3*	12.82	43.8	10.83	43.7	12.16	18.0	10.49	12.7	13.29	33.2	11.13	22.8	11.44
20.4	12.21	32.5*	12.65	42.0	9.79	40.5	12.18	14.1	10.43	11.2*	13.27	31.9	11.02	20.3	11.15
18.9	11.71	31.0*	12.84	41.1	10.20	38.5	13.61	12.4	10.41	10.0	13.02	30.5	10.73	18.3*	11.29
17.0	12.19	29.5	12.53	39.9	9.74	34.7	12.36	10.7	10.32	8.6	13.64	29.1	10.69	16.1	11.91
15.4	12.46	28.0*	13.19	38.7	10.41	31.6	12.12	9.2	9.84	7.0*	13.56	27.6	10.21	14.1	11.79
11.6	12.66	26.5**	12.88	37.5*	10.19	28.4	12.25	7.7	9.85	5.3	13.29	26.4	10.69	12.3	11.59
9.2*	12.13	24.8*	13.01	36.7	9.62	25.5	11.16	5.5	9.92	3.7	13.49	25.0	10.44	10.1	12.03
7.6	11.39	23.2*	13.22	34.9	9.32	22.4	11.77	4.0	10.61	2.0	13.31	23.4	10.40	7.9	11.57
6.0	11.67	21.3*	13.60	33.4	9.17	19.2	11.39	1.7	10.48	0.0	13.37	22.2*	10.67	5.4	11.47
3.8	11.21	19.7*	13.18	32.3	10.70	15.7	11.67	0.0	9.85			19.2	10.73	2.7*	11.50
2.0	11.93	18.0*	12.68	29.8	9.98	11.4	12.33					18.0	10.19	0.0	11.53
0.0	11.78	15.7*	12.70	28.5	10.53	8.2	11.86					16.6	10.81		
		14.0*	12.87	27.8	10.56	4.2	13.46					14.4	10.54		
		12.1*	12.57	26.7	10.89	0.0	11.25					13.1	10.47		
		9.2	12.42	25.5*	11.07							11.7	10.55		
		7.3**	12.36	23.8	10.49							10.0*	10.49		
		5.8*	12.42	22.2	10.96							8.1	10.59		
		3.8*	12.09	19.3	11.02							6.5	10.41		
		2.3*	11.78	16.5	10.79							4.9	10.68		
		0.0*	11.67	14.8	11.76							3.8	10.27		
				13.2	10.64							2.1	10.67		
				11.5	10.28							0.0*	10.83		
				10.0	10.77										
				8.5	9.65										
				7.0*	10.81										
				5.7	10.41										
				3.9	10.04										
				3.0	9.85										
				1.2	9.58										
				0.0	9.87										

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