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Microscale $\delta^{18}O$ and $\delta^{13}C$ isotopic analysis of an ontogenetic series of the hadrosaurid dinosaur *Edmontosaurus*: implications for physiology and ecology

Kathryn J. Stanton Thomas*, Sandra J. Carlson

Department of Geology, University of California, Davis, CA 95616, USA

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Abstract

Stable isotope analysis of vertebrate biominerals, primarily in mammals, has been used to address questions of paleodiet, paleoclimate, trophic level, migration, foraging zone, and thermophysiology with varying degrees of success. Isotopes have been used less commonly to study physiology and ecology through ontogeny in dinosaurs, generally due to (1) the lack of modern analogs as a basis for comparison of observed fossil isotope values, and (2) difficulty in sampling very thin tooth enamel (a non-remodeled biomineral). By utilizing a relatively new technique in microsampling, this study addresses the following questions: Do microscale analyses of oxygen and carbon isotopes from mineralized tissues of hadrosaurid dinosaurs record temporal variation? If so, is the cause of the variation physiological or ecological?

Isotope values from the carbonate component of enamel ($\delta^{18}O_{ec}$ and $\delta^{13}C_e$) were obtained by microsampling multiple teeth in a temporal series from the dental batteries of a juvenile, sub-adult, and adult *Edmontosaurus* from the Late Cretaceous Maastrichtian Hell Creek Formation of South Dakota. To establish isotope variability in an extant archosaur, consecutive teeth in a temporal series from an extant *Alligator mississippiensis* specimen were microsampled for isotopic analysis and compared to those of *Edmontosaurus*. To test for diagenesis, bulk samples from the phosphate component ($\delta^{18}O_p$) of modern and fossil tooth enamel, bone, and dentine from *Edmontosaurus*, *A. mississippiensis*, and extant ratites were analyzed and compared. *Edmontosaurus* bone and dentine indicate a greater degree of alteration than does enamel, and while absolute $\delta^{18}O_{ec}$ values may be altered, the pattern of seasonal cycles appears to be preserved and can provide detailed information on hadrosaur physiology (tooth mineralization times, rates, and seasons) and ecology (dietary information).

$\delta^{18}O_{ec}$ seasonal patterns are preserved in *Edmontosaurus* specimens, and are interpreted to correlate with annual $\delta^{18}O$ variation of local meteoric waters rather than thermophysiology, changes in drinking water sources, or migration. All teeth were mineralized in < 0.65 year with no consistent season of mineralization. Mean tooth mineralization times are shorter in the juvenile and sub-adult than the adult. Enamel mineralization rates are estimated to be $\sim$ 38 mm/year in *Edmontosaurus* and $\sim$ 36 mm/year in *Alligator* (consistent with mineralization rates for modern ungulates), although the length of time for tooth formation is shorter in the archosaurs compared with mammals. Heavier than predicted $\delta^{13}C_e$ values are hypothesized to result from (1) enrichment of $\delta^{13}C$ in ingested plant material due to higher atmospheric $\delta^{13}C$ ($\delta^{13}C_{atm}$) in the Late Cretaceous; (2) taxon-specific $\delta^{13}C$ effects of ingested plants (primarily gymnosperms); (3) isotopic enrichment of ingested plant material ($\delta^{13}C_p$) due to osmotic stress from proximity to the Western Cretaceous Interior Seaway, (4) taxon-specific $\delta^{13}C_{diet}-\delta^{13}C_e$ fractionation factors for *Edmontosaurus* that vary from those observed in modern mammals, and/or (5) diagenesis. Microsampling provides a detailed

* Corresponding author. Tel.: +1-530-752-0350; fax: +1-530-752-0951.
E-mail address: Stanton@geology.ucdavis.edu (K.J. Stanton Thomas).

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perspective on the physiological (tooth mineralization times, rates, and seasons) and ecological (dietary) mechanisms of oxygen and carbon isotope incorporation in dinosaur biominerals that is not obtainable through bulk sampling alone.

Keywords: Carbon and oxygen stable isotopes; Enamel; Teeth; Dinosaurs; Diagenesis

1. Introduction

Over the last 20 years stable isotope analysis of vertebrate biominerals has emerged as a powerful tool for investigating questions regarding environmental and physiological variation in extinct organisms, especially mammals (Kolodny and Luz, 1991; Quade et al., 1992; Barrick and Showers, 1994; Bryant et al., 1994; Cerling and Sharp, 1996; Kolodny et al., 1996; Longinelli, 1996; MacFadden and Cerling, 1996; Koch et al., 1998; Sharp and Cerling, 1998; Feranec and MacFadden, 2000; Fricke and Rogers, 2000; Thomas and Carlson, 2001). Oxygen isotopes are used to study paleoenvironments (because they reflect seasonal variation in temperature and humidity, latitude, and precipitation) and physiology (because they undergo a temperature-dependent biological fractionation in animals; Fig. 1A). Carbon isotopes are valuable for determining ecological information such as diet, niche partitioning, and trophic level because they undergo differential fractionation during photosynthesis and therefore reflect plant type preferences in herbivores (reviewed in Koch, 1998; Kohn and Cerling, 2002; Fig. 1B).

Whereas stable isotope geochemistry is widely used to study fossil mammals, the same is not true of fossil, non-avian dinosaurs. Interpretation of geochemical data from dinosaur enamel is complicated by factors such as diagenetic alteration (Nelson et al., 1986; Kolodny et al., 1996; Longinelli, 1996; Goodwin and Bench, 2000); difficulty in interpreting isotopic signals in a group of extinct and physiologically perplexing animals; the difficulty of sampling very thin tooth enamel (<200 μm, this study), which is the only permanent, non-remodeled mineralized vertebrate tissue available (Noyes et al., 1938; Lowenstam and Weiner, 1989; Carlson, 1990); and the lack of a continuous long-term isotopic record from a single individual, because dinosaurs continually shed teeth throughout life (Owen, 1840-45; Edmund, 1960). Consequently, it has been difficult for researchers using isotope techniques to reconstruct the physiology (e.g. changes in growth rate or timing in teeth) and

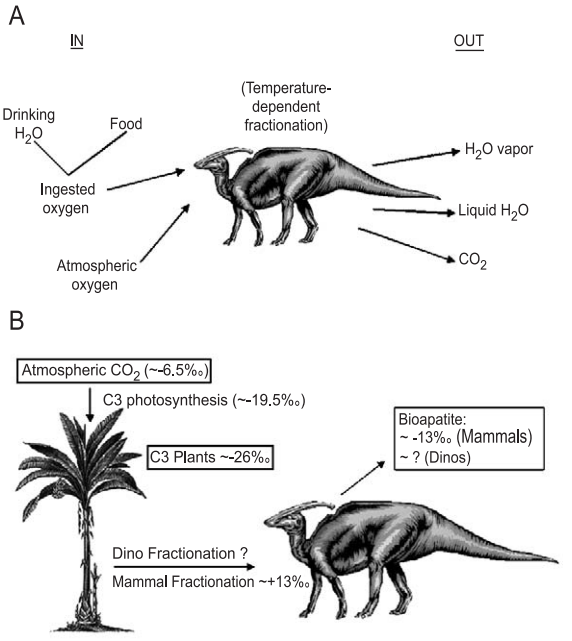


Fig. 1. Variables affecting $\delta^{18}O$ and $\delta^{13}C$ in enamel, dentine, and bone in terrestrial vertebrates. (A) Inputs and outputs of oxygen isotopes, which are primarily affected by a temperature-dependent physiological fraction of $\delta^{18}O$ of ingested oxygen from food and drinking water (Luz and Kolodny, 1989). Inspired atmospheric oxygen has a relatively invariant isotopic composition (Hoefs, 1997) and therefore contributes little to isotopic variability in bioapatites. Modified from Barrick (1998). (B) Inputs and outputs of carbon isotopes, which are a reflection of atmospheric CO_2, fractionation during photosynthesis, and physiological fractionation (which is well-understood in mammals and unknown in dinosaurs). Modified from Koch (1998).

ecology (e.g. diet) of dinosaurs over an extended time span of months to years, throughout ontogeny.

Although dinosaurs are known to have replaced their teeth many times throughout life, hadrosaurid (''duck-billed'') dinosaurs (including *Edmontosaurus*, the genus used in this study) possess a broad pavement of interlocking teeth called a dental battery (Fig. 2). The dental battery consists of up to five teeth stacked vertically in one tooth position (or column; Ostrom, 1961), with columns interlocking side by side. As teeth were worn, deeper rows erupted continuously to form an occlusal surface for grinding food. Enamel from successive tooth rows in this dental battery therefore represents a long-term non-remodeled surface suitable for isotopic analysis of growth rates.

In this study, we use stable isotopes to explore several questions related to dinosaur ontogeny. First, does hadrosaur tooth enamel retain a primary environmental seasonal oxygen isotopic composition—and if so, does this signal vary ontogenetically—within a single tooth, among teeth in one individual, and among individuals of different ages? Second, do oxygen and carbon isotopes from successive microscale samples of mineralized tissues of the Late Cretaceous hadrosaurid dinosaur *Edmontosaurus* vary seasonally? If so, is the cause of the variation physiological, ecological (seasonal), or diagenetic? Third, can oxygen isotopes be used to estimate tooth mineralization rates and tooth formation times in this genus, and is the season of mineralization consistent? Finally, does hadrosaur tooth enamel retain a primary carbon isotope signal, and if so, what dietary information can be obtained from $\delta^{13}C_e$? We analyze modern *Alligator* enamel in order to establish a baseline for comparison to the extinct dinosaurs. We also perform an analysis of diagenetic alteration by isotopic comparison of *Edmontosaurus* bioapatite to bioapatites from some of its closest living relatives, *Struthio* (Ostrich), *Rhea*, and *Alligator*.

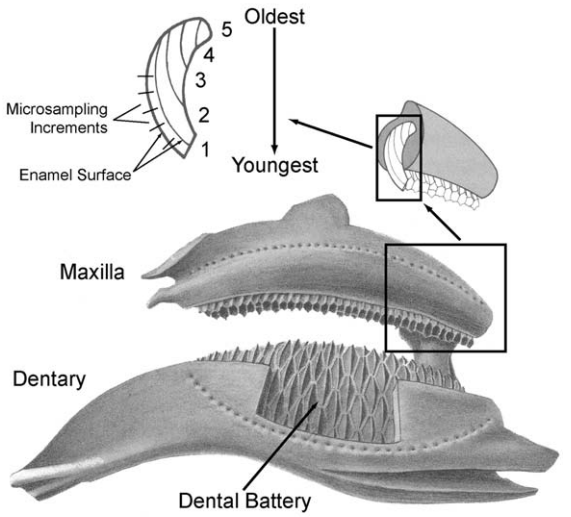


Fig. 2. Hadrosaurid dental battery showing detail of sectioned maxilla and microsampling increments for individual teeth within each jaw. Oldest (i.e. tooth #1, erupted, at occlusal surface) to youngest teeth (i.e. tooth #5, un-erupted within jaw) are micro-drilled along sampling increments from the occlusal surface up to collect enamel powder for $\delta^{18}O_{ec}$ and $\delta^{13}C_e$ analysis (enamel is mineralized on only one side of each tooth in hadrosaurs). After sampling, sections are re-ground, polished, and re-sampled multiple times in order to collect enough enamel powder for isotopic analysis. Sampling in this manner from an ontogenetic series allows for temporal reconstruction of patterns of isotopic incorporation in this dinosaur. Modified from Horner and Gorman (1988).

Previous analyses of environmental (seasonal) patterns from microsampled enamel have focused on mammals to: (1) track environmental responses in modern enamel isotopes to changes in temperature, humidity, and precipitation (Stuart-Williams and Schwarz, 1997; Fricke et al., 1998a; Lindars et al., 2001), and (2) apply knowledge of modern enamel isotope patterns to the fossil record in paleoclimate studies (Koch et al., 1989, 1998; Fricke and O'Neil, 1996; Fricke et al., 1998b; Sharp and Cerling, 1998; Feranec and MacFadden, 2000). Previous isotope studies of dinosaur bone and enamel have focused on inter- and intra-bone and enamel isotopic variability to determine whether dinosaurs are endothermic or ectothermic (Barrick and Showers, 1994, 1995, 1998; Barrick et al., 1996, 1998; Fricke and Rogers, 2000).

This study represents one of the first attempts to conduct a micro-scale study of carbon and oxygen isotopes from a monogeneric dinosaurian ontogenetic series using a relatively new technique for incremental microsampling of very thin tooth enamel (see also Straight et al., this volume). As such, it provides a detailed ontogenetic perspective on cyclical oxygen and carbon isotope variations and their relationship to dinosaur physiology (tooth mineralization rates, tooth

formation times, and season of tooth mineralization) and dietary preferences.

2. Biomineralization

2.1. Bioapatite structure and diagenesis

Vertebrate bioapatites (bone, dentine, and enamel) are composed of $Ca_5(PO_4)_3OH$ (carbonate hydroxylapatite, or dahllite) mineralized on an organic framework (Lowenstam and Weiner, 1989). In vivo ionic substitutions are common in the bioapatite crystal lattice, including the substitution of carbonate (4–6% by weight) for phosphate (LeGeros et al., 1967; McConnell, 1973; LeGeros, 1981; Carlson, 1990). Ionic substitutions can also occur postmortem in the form of diagenetic alteration by one of two processes. First, chemical replacement of original bioapatite can result in replacement of the original CO_3^{2-} and/or PO_4^{3-}, and/or elemental enrichment in U, rare earth elements, F, and Sr (Nelson et al., 1986; Grandjean and Albarède, 1989; Tuross et al., 1989; Toyoda and Tokonami, 1990; Kohn et al., 1999). Second, precipitation of secondary minerals on bioapatite through water–fossil interactions can result in elemental enrichment of, e.g. Fe, Mn, Al, Si, Ba, and Cu (Dauphin, 1991; Kohn et al., 1999; Sponheimer and Lee-Thorp, 1999; Goodwin and Bench, 2000).

Bone (including cortical, or compact, and cancellous, or spongy types) and dentine have a higher organic content ($\sim$ 30 wt.% in bone/dentine vs. often $<$ 1 wt.% in enamel), smaller crystallites, and higher porosity than does enamel (Hillson, 1986; Lowenstam and Weiner, 1989; Carlson, 1990). Bone and dentine are "remodeled" via dissolution and reprecipitation throughout life; enamel is deposited by accretion and is not remodeled (Lowenstam and Weiner, 1989). Because of these structural differences, enamel is more resistant to diagenetic alteration and is therefore preferable to bone and dentine in isotopic analyses (e.g. Lee-Thorp and van der Merwe, 1987; Carlson, 1990; Thackeray et al., 1990; Quade et al., 1992; Ayliffe et al., 1994; Wang and Cerling, 1994; Iacumin et al., 1996; Koch et al., 1997). To answer questions about fossils as living organisms, it must be demonstrated that original isotopic signatures have been preserved (Nelson et al., 1986; Kolodny et al., 1996; Kohn et al., 1999; Sponheimer and Lee-Thorp, 1999).

2.2. Sources of oxygen isotopes

Oxygen for isotopic analysis is obtained from either the PO_4^{3-} or the CO_3^{2-} ion in bioapatite (Tudge, 1960; Kolodny et al., 1983; Quade et al., 1992; O'Neil et al., 1994). Phosphate oxygen is less prone to diagenetic alteration than is carbonate oxygen because of stronger chemical bonds in the compound (Bryant et al., 1996; Barrick, 1998; Kohn et al., 1999), although it is by no means immune (Ayliffe et al., 1994; Kolodny et al., 1996; Blake et al., 1997). Oxygen from PO_4^{3-} requires relatively large sample sizes ($\sim$ 0.7 mg), limiting its use in microscale analyses. Conversely, carbonate oxygen ($\delta^{18}O_c$; see Table 1 for summary of all δ notation abbreviations) can be analyzed from smaller samples ($\sim$ 0.15 mg) and is therefore more appropriate for microsampled bioapatite. Carbonate isotope analysis has better analytical precision than does PO_4^{3-}, and $\delta^{13}C$ from the carbonate component of bioapatite is obtained at the same time as $\delta^{18}O_c$, whereas $\delta^{13}C$ is not obtained during $\delta^{18}O_p$ isotope analysis (Bryant et al., 1996). Its greatest disadvantage is that CO_3^{2-} is more prone to diagenesis than is PO_4^{3-} (Wang and Cerling, 1994; Sponheimer and Lee-Thorp, 1999), which limits its use to very well-preserved fossil specimens.

Table 1
Summary of abbreviations for all delta notations within text

Abbreviation	Isotope derived from:
$\delta^{18}O_c$	Enamel, dentine, or bone carbonate
$\delta^{18}O_{bc}$	Bone and/or dentine carbonate
$\delta^{18}O_{ec}$	Enamel carbonate
$\delta^{18}O_p$	Enamel, dentine, and/or bone phosphate
$\delta^{18}O_{bp}$	Bone and/or dentine phosphate
$\delta^{18}O_{ep}$	Enamel phosphate
$\delta^{18}O_{water}$	Meteoric water
$\delta^{13}C_b$	Bone and/or dentine
$\delta^{13}C_e$	Enamel carbonate
$\delta^{13}C_{atm}$	Atmospheric CO_2
$\delta^{13}C_{diet}$	Diet
$\delta^{13}C_p$	Plant tissues
$\delta^{13}C_{oc}$	Sedimentary organic carbon
$\Delta^{18}O_p$	Enamel, dentine, and/or bone phosphate[a]
$\Delta^{18}O_{ec}$	Enamel carbonate[a]
$\Delta^{18}O_c$	Enamel, dentine, and/or bone carbonate[a]
$\Delta^{13}C_e$	Enamel carbonate[a]

[a] $\Delta=(\delta_{high}-\delta_{low})$ values.

3. Materials and methods

3.1. Specimens

Three maxillae with intact dental batteries were obtained from the Concordia *Edmontosaurus* bonebed in the Hell Creek Formation, located south of Morristown near the Grand River, in Corson County, South Dakota. The Hell Creek Formation represents Late Cretaceous (Maastrichtian) fluvial nonmarine sediments that were laid down on the western margin of the Western Cretaceous Interior Seaway. Sediments include sandstones, siltstones and mudstones representing channel and floodplain deposits (Lofgren, 1997). This formation contains a wide variety of vertebrate fossils, including dinosaurs (ornithopods, pachycephalosaurs, ankylosaurs, ceratopsians, and theropods; (Weishampel, 1990), turtles, mammals (e.g. Archibald, 1977), and crocodiles (Estes et al., 1969).

The bonebed sediments record a ''marine-terrestrial transition from shoreface and foreshore environments to the complex system of coastal dunes, coastal swamps, and distributary channels that formed during the progradation of the Hell Creek sediments into the Cretaceous Fox Hills seaway'' (R. Nellermoe, 2002, personal communication). The bonebed itself is interpreted to have been deposited in a pervasive coastal swamp to fluvial-dominated distributary transition.

Three maxillae of different sizes, presumed to represent an ontogenetic series (juvenile, 28.5 cm; sub-adult, 34 cm estimated length; and adult, 42 cm) of the hadrosaurid dinosaur *Edmontosaurus* were transversely sectioned using a diamond blade cut-off saw. Sectioned ends of the maxillae were impregnated with Silmar resin in vacuo to stabilize loose teeth within the jaws, and sections were subsequently ground and polished. Comparisons between resin-contaminated bioapatite and uncontaminated samples demonstrate that neither bone phosphate oxygen ($\delta^{18}O_{bp}$) or bone carbonate oxygen ($\delta^{18}O_{bc}$) are affected by resin impregnation.

In addition to the dinosaur specimens, a femur and tibia from the modern African ostrich (*Struthio camelus*, UCMP-125001) and a domestically raised Rhea (*Rhea americana*, UCMP 129668) were obtained from the University of California Museum of Paleontology, and a skull from a wild-caught specimen of *Alligator mississippiensis* was obtained from the Louisiana Department of Wildlife and Fisheries. Isotope values from these ratite (*Struthio* and *Rhea*) and alligator specimens were used for comparison to isotope values from *Edmontosaurus* enamel, dentine, and bone in the evaluation of diagenetic alteration in the *Edmontosaurus* specimens. Additionally, two pairs of erupted teeth and their un-erupted replacements (four teeth total) were removed from the *Alligator* specimen for microscale isotopic comparison to *Edmontosaurus* teeth (see Results and Discussion).

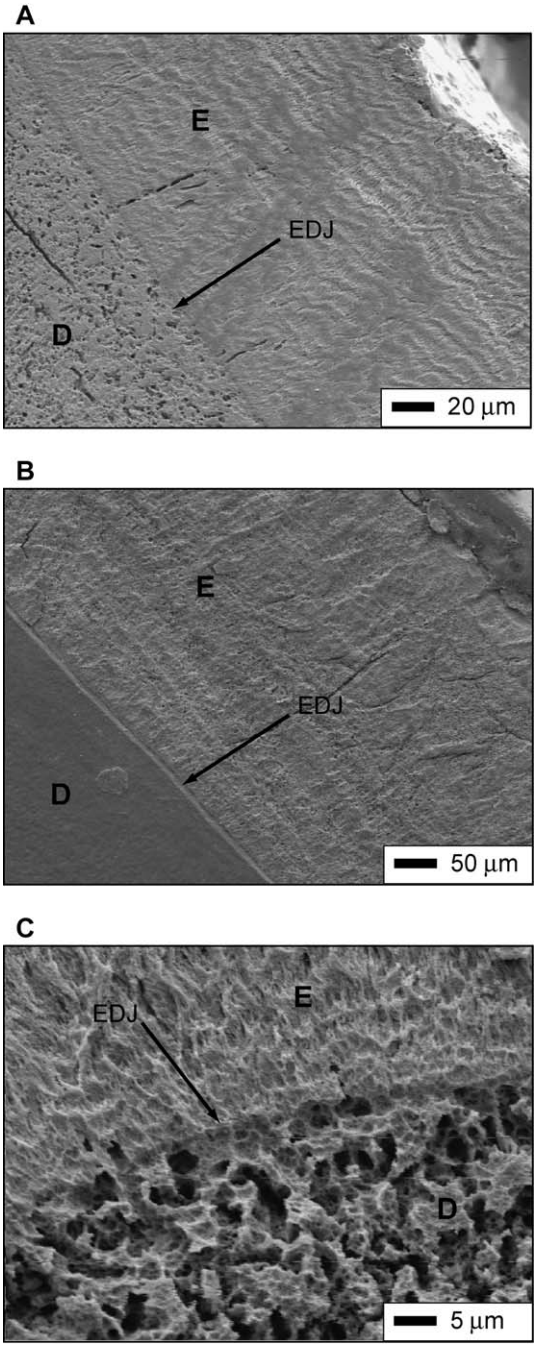
3.2. Scanning electron microscopy

A single, partially erupted and worn tooth from *Edmontosaurus* (specimen CC-MN-211) was removed from the dental battery, longitudinally and transversely sectioned, and acid-etched in 10% HCL for 5–10 s in order to expose the crystalline apatite microstructure (Sander, 2000). A single erupted tooth from *A. mississippiensis* was treated in the same manner. Sections of both teeth were coated with gold and examined using scanning electron microscopy (SEM) to (1) verify that the original crystalline microstructures were preserved in the *Edmontosaurus* specimen (see Results), (2) identify the enamel–dentine junction (EDJ) in both species, and (3) ascertain average enamel thickness in both specimens (Fig. 3).

3.3. Sampling for isotopic analysis in Edmontosaurus enamel

Enamel crystallites in non-mammalian amniotes (reptiles, toothed birds, and mammal-like reptiles) grow either normal to or at a generally high angle to the EDJ (Scott and Symons, 1971; Sander, 1997). As a result, growth lines in these taxa are also normal or at an angle to the EDJ. Because of this characteristic growth, enamel sampled down the length of a tooth (from crown to root) will cross progressively younger enamel in a temporal series. Hadrosaurids (including *Edmontosaurus*) and *Iguanodon* uniquely possess *wavy enamel* (Sander, 2000), which lacks incremental lines and has a distinctive appearance under SEM. Although lacking obvious growth lines, we assume that *Edmontosaurus* enamel retains the same growth pattern (normal or at a high angle to the EDJ) observed in other non-mammalian amniotes, and that tooth enamel sam-

pled from crown to root in *Edmontosaurus* represents a temporal sequence of enamel mineralization, as it does in other vertebrates.



Edmontosaurus enamel from four teeth from a single growth column in each of the three dental batteries (CC-MN-207, CC-MN-2070, CC-MN-1448) was sampled using an automated Merchantek microdrilling system. Sequential samples 50 µm wide and ~ 50 µm deep were collected along each tooth from crown to root, resulting in between one (for the smallest/youngest teeth) and six (for larger/older teeth) samples per tooth (Table 2, Fig. 2). Throughout the text, the oldest (i.e. erupted) teeth are designated "0" or "1," and subsequent replacement teeth are labeled 2, 3, or 4 with decreasing tooth age (Fig. 2). Subsequent to this initial microsampling of all teeth in a single section, the section was again ground, polished, and each tooth re-sampled (using the same sampling increments), with subsequent samples from each section added to the original until a sufficient amount of sample (150–200 µg) was obtained (Fig. 2) for isotopic analysis. The samples were then roasted in vacuo at 375 °C for 35 min to reduce organic matter, and reacted with supersaturated (105%) H_3PO_4 at 90 °C using a common acid bath Isocarb device. The resulting CO_2 was analyzed for $\delta^{18}O_{ec}$ and $\delta^{13}C_e$ on an attached Fisons Optima Isotope Ratio Mass Spectrometer (IRMS) at the University of California, Davis. Based on repeated analyses of internal standards, precision of the measurements is ±0.04 and ±0.06 ‰ for C and O, respectively.

For 7 of the 12 microsampled *Edmontosaurus* teeth, larger (bulk) samples of enamel (~ 0.3 to 1.0 mg, typically 1 sample per tooth) were also collected for phosphate oxygen analysis (which requires larger samples than does carbonate oxygen analysis) using the Merchantek microdrilling system. These bulk samples were dissolved in HF and reprecipitated as Ag_3PO_4 using the rapid-precipitation method of Dettman et al., (2001; modified from O'Neil et al., 1994). Samples were converted to CO using a EuroVector elemental analyzer (EA) at 1270 °C in the presence of glassy carbon. The CO was subsequently introduced

Fig. 3. Scanning electron micrographs of *Edmontosaurus* and modern *Alligator* enamel and dentine, showing the enamel–dentine junction (EDJ). (A) *Edmontosaurus* enamel ("E," upper right half of image); dentine ("D") in lower left. Note "wavy" enamel, apparently unique to the clade comprising the Hadrosauridae and Iguanodontidae (Sander, 2000). (B) *Alligator* enamel in upper right half of image; dentine in lower left. (C) *Edmontosaurus* enamel, close-up of EDJ; enamel is in upper left portion of image, with much lower-density dentine in lower right.

Table 2
Summarized results of oxygen ($\delta^{18}O_{ec}$) and carbon ($\delta^{13}C_e$) from enamel carbonate of all microsampled teeth (*Edmontosaurus* and modern *Alligator*)

Specimen	Tooth	No. of samples per tooth	Mean			Mean		
			Intra-tooth $\delta^{18}O_{ec}$ (‰)	S.D.[a]	Intra-tooth $\Delta^{18}O_{ec}$ (‰)[b]	Intra-tooth $\delta^{13}C$ (‰)	S.D.[a]	Intra-tooth $\Delta^{13}C_e$ (‰)[b]
Edmontosaurus								
Juvenile	1	6	20.9	2.1	4.9	− 2.7	1.1	2.4
(CC-MN-207)	2	4	19.3	0.7	1.5	− 3.8	0.5	1.2
	3	2	19.3	0.4	0.5	− 4.4	0.7	0.9
	4	1	19.2	n/a	n/a	− 4.2	n/a	n/a
Sub-adult	0	2	19.8	1.3	1.8	− 3.0	0.8	1.2
(CC-MN-1448)	1	3	18.8	0.8	1.7	− 3.3	0.1	0.1
	2	4	19.2	1.0	2.2	− 1.7	1.2	2.8
	3	3	18.9	1.4	2.5	− 2.0	1.7	3.2
Adult	1	5	19.1	0.5	1.3	− 4.5	0.4	1.0
(CC-MN-2070)	2	5	17.6	0.7	1.8	− 6.2	0.6	1.5
	3	4	17.9	0.3	0.6	− 6.7	0.5	1.0
	4	3	20.0	0.8	1.6	− 4.4	0.8	1.7
Mean[c]			19.2	1.3	1.8	− 4.0	1.7	1.5
Total range of all specimens			6.1			7.0		
Alligator								
No. 7[d]	A	6	24.7	0.3	0.8	− 14.0	0.5	1.3
	B	3	24.2	1.0	1.9	− 12.2	0.2	0.5
No. 8[d]	A	6	24.7	0.4	1.0	− 14.3	0.7	1.9
	B	5	24.6	0.9	2.3	− 12.1	0.2	0.4
Mean[c]			24.6	0.6	1.5	− 13.4	1.1	1.0
Total range of all specimens			2.3			3.3		

Results are given in permil (‰) notation, with oxygen isotopes relative to VSMOW and carbon isotopes relative to VPDB. External precision for carbonate analyses is accurate to hundredths; however, for consistency with reported phosphate oxygen values (see Appendix A), all isotope values are reported to tenths.

[a] Standard deviation of mean intra-tooth δ values.

[b] $(\delta_{high} - \delta_{low})$ values for each tooth.

[c] Calculated using entire data set.

[d] Both pairs of teeth (7 and 8) from same specimen.

into a Micromass Isoprime IRMS in a He stream, where it was analyzed for enamel phosphate oxygen ($\delta^{18}O_{ep}$) (Table 2) at the U.S. Geological Survey Stable Isotope Laboratory in Menlo Park, CA.

Results of all isotopic analyses are reported in standard notation, $\delta X(‰) = (R_{sample}/R_{standard} - 1) \times 10^3$, where R is the ratio of $^{18}O/^{16}O$ or $^{13}C/^{12}C$ relative to the international standards Vienna Standard Mean Ocean Water (VSMOW for $\delta^{18}O$) or Vienna Pee Dee belemnite (VPDB for $\delta^{13}C$; Table 2). Results for $\delta^{18}O_p$ are reported as the mean of two replicate analyses from the same sample. Due to limited enamel sample availability, microsampled $\delta^{18}O_{ec}$ values are reported from single samples. Precision of $\delta^{18}O_p$ measurements is ±0.3 ‰, based on repeated analyses of 90 standards.

3.4. Other sampled material

In addition to enamel, samples of both cancellous and cortical bone and dentine were drilled from the *Edmontosaurus* maxillae using No. 701 taper/flat end crosscut carbide dental burs. In addition to the three maxillae with intact teeth that were sampled, a fourth maxilla (CC-MN-211) was bulk sampled only for bone. These bone and dentine samples were analyzed isotopically for phosphate oxygen ($\delta^{18}O_{bp}$), bone carbonate oxygen ($\delta^{18}O_{bc}$), and bone carbon ($\delta^{13}C_b$) using the same analytical techniques as on the *Edmontosaurus* enamel (see Appendix A).

Small (~ 1 cm^2) pieces of modern *Struthio* (ostrich) tibia and femur (UCMP-125001) and *Rhea* femur

(UCMP-129668) were removed from whole bones using a Foredom™ flexible-shaft tool and 1-7/8" Damascus separating disks. The bone cores were subsequently serially sectioned, ground, and pre-treated to remove organic matter (sonicated and soaked overnight in 2–3% NaOHCl, rinsed, then sonicated and soaked overnight in 0.125N NaOH, rinsed, and dried) (Koch et al., 1997). Splits of each ground section were roasted and subsequently analyzed for $\delta^{18}O_{bc}$, $\delta^{18}O_{bp}$, and bone carbon ($\delta^{13}C_b$) using the same methods described for the *Edmontosaurus* specimens (Table 2).

Two pairs of erupted teeth and their pre-eruptive replacements (four teeth total) were removed from the skull of a large (2.25 to 2.4 m snout to tail), wild specimen of *A. mississippiensis* from Louisiana. The teeth were mounted to glass slides and sectioned using a Buehler Isomet low speed saw. All teeth were microsampled for enamel in the same manner as were the *Edmontosaurus* teeth. These samples were not pretreated as this has been shown to have no significant effect on enamel $\delta^{18}O_{ec}$ values (Koch et al., 1997) because enamel contains < 1% organic material (Hillson, 1986; Lowenstam and Weiner, 1989; Carlson, 1990). Samples were roasted and isotopically analyzed for $\delta^{18}O_{ec}$ and $\delta^{13}C_e$ using the same methods as those for the *Edmontosaurus* specimens (Table 2).

4. Results

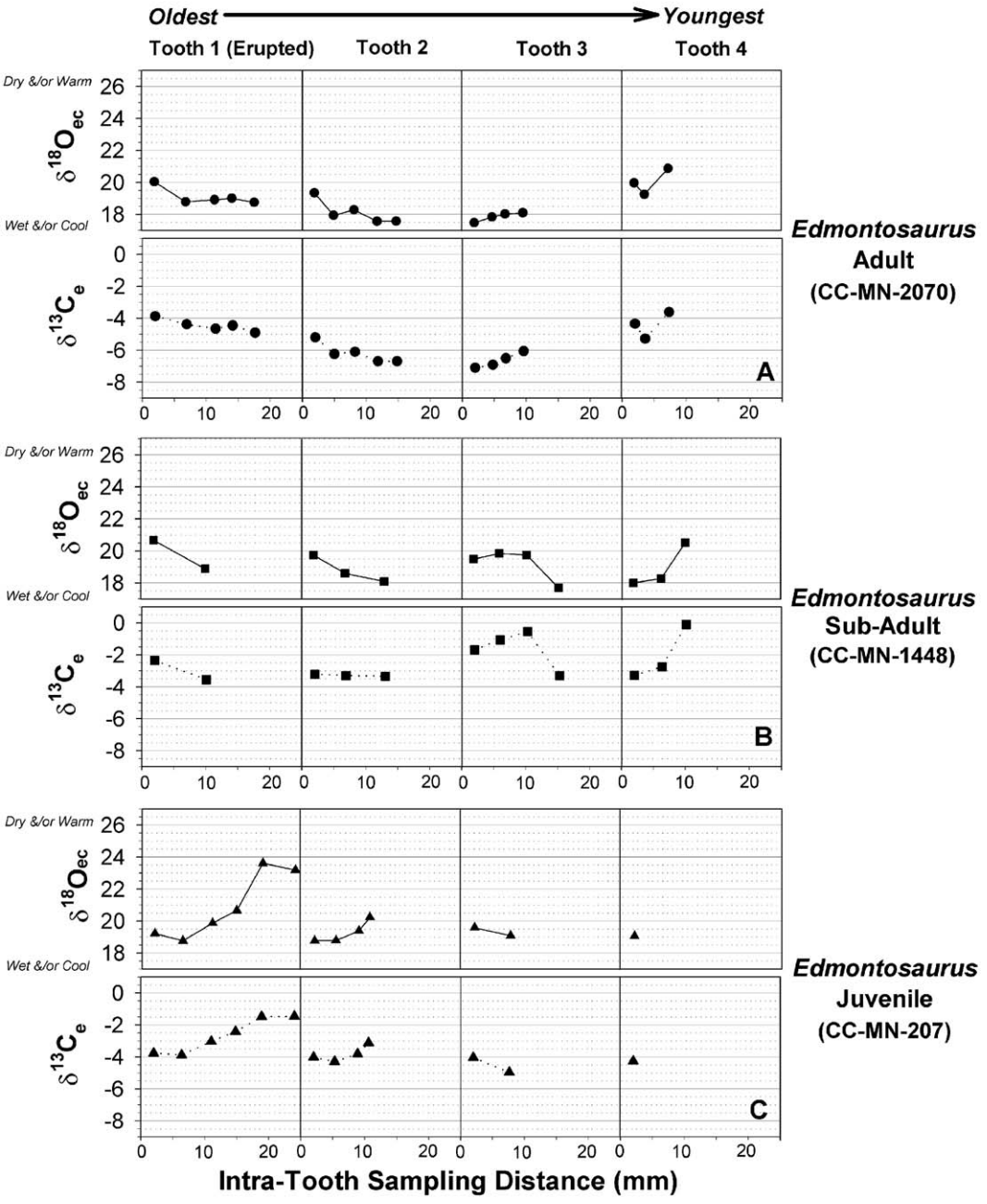
4.1. Oxygen isotopes from microsampled teeth

As mentioned, sampling increments in individual teeth may be used as a proxy for temporal variation (vertebrate teeth are mineralized from crown to root, so that crown enamel is oldest and enamel near the root is youngest; Fig. 2). Thus, increases and/or decreases in $\delta^{18}O_{ec}$ within a single tooth represent changes in the $\delta^{18}O$ values of the inputs (ingested food or water) during the time of tooth mineralization (Fig. 1A). All teeth with >1 enamel sample from all three *Edmontosaurus* jaws show a pattern of gradual temporal variation (either increase or decrease) in $\delta^{18}O_{ec}$ values (Fig. 4A, B, C, F). For instance, $\delta^{18}O_{ec}$ in the adult specimen (CC-MN-2070; Fig. 4A, upper plot) shows generally decreasing values from the crown to the root in tooth #1 and #2, versus increasing crown to root $\delta^{18}O_{ec}$ values in tooth #3. Tooth #4 shows a decrease and then an increase in $\delta^{18}O_{ec}$, although only three samples were available from this tooth, which makes identification of a trend difficult. Similar patterns of sequential increase or decrease (rather than oscillations) are apparent in the *Alligator* specimen (Fig. 4D, E). These patterns closely resemble temporal $\delta^{18}O_{ec}$ variation observed in modern mammal teeth, in which $\delta^{18}O_{ec}$ values track cyclical (seasonal) variation in $\delta^{18}O_{water}$ (Koch et al., 1989, 1998; Fricke and O'Neil, 1996; Stuart-Williams and Schwarz, 1997; Fricke et al., 1998a; Kohn et al., 1998; Sharp and Cerling, 1998; Feranec and MacFadden, 2000; Wurster and Patterson, 2001; Passey and Cerling, 2002). Results of isotopic analyses for all microsampled teeth from the *Edmontosaurus* and *Alligator* specimens are summarized in Table 2. Plots of $\delta^{18}O_{ec}$ and $\delta^{13}C_e$ versus sampling increment for *Edmontosaurus* and *Alligator* are shown in Fig. 4.

Intra-tooth variability ($\Delta^{18}O_{ec}$) for all microsampled *Edmontosaurus* teeth ranges from 0.5‰ to 4.9‰

Fig. 4. Plots of $\delta^{18}O_{ec}$ and $\delta^{13}C_e$ versus intra-tooth sampling distance. Distances given are measured from the crown of each tooth. Solid lines between samples represent $\delta^{18}O_{ec}$, dotted lines are $\delta^{13}C_e$. External precision for isotope values is within the size of the symbols. (A) Black circles, adult *Edmontosaurus* specimen (CC-MN-2070); (B) black squares, sub-adult *Edmontosaurus* specimen (CC-MN-1448); (C) black triangles, juvenile *Edmontosaurus* specimen (CC-MN-207); (D) open diamonds, modern *Alligator* (teeth 7A,B, an erupted tooth and its replacement); (E) open hexagons, modern *Alligator* (teeth 8A,B, a second erupted tooth and its replacement); (F) all *Edmontosaurus* and *Alligator* teeth plotted together. In vertebrate teeth, enamel mineralization proceeds from crown (oldest) to root (youngest) (Carlson, 1990), so that microsamples taken along the length of the enamel represent a temporal series of enamel mineralization within a single tooth (Fig. 2). Multiple teeth within a single jaw were sampled in this manner, and teeth are plotted from oldest tooth sampled (#1, at the occlusal surface) to youngest (un-erupted) within a single individual. For *Edmontosaurus*, three individuals in an ontogenetic sequence were sampled. As such, this plot represents a hierarchical record of isotope incorporation through an ontogenetic series of *Edmontosaurus*. We assume in this study that sampling distance has a relationship to temporal incorporation of isotopes, although the precise nature of the relationship is not known. We therefore base our calculations of tooth formation times and enamel mineralization rates on a 6-month cool/wet and 6-month warm/dry seasonality (see Discussion). Variation from this assumed ratio of cool/wet to warm/dry seasons would be difficult to assess from the data in this study because teeth were mineralized in < 1 complete seasonal cycle (see Koch et al., 1989; Fricke and O'Neil, 1996; Stuart-Williams and Schwarz, 1997; Fricke et al., 1998a; Kohn et al., 1998; Sharp and Cerling, 1998 for related studies).

(Table 2, Fig. 5B), comparable to the 1–6 ‰ $\Delta^{18}O_{ec}$ that exists in extant mammals (Fricke and O'Neil, 1996; Stuart-Williams and Schwarz, 1997; Fricke et al., 1998a; Kohn et al., 1998, 1999; Sharp and Cerling, 1998). $\Delta^{18}O_{ec}$ for the *Alligator* specimen is somewhat smaller, ranging from 0.8 ‰ to 2.3 ‰ (Table 2; Fig. 5B), comparable to $\Delta^{18}O_{ec}$ in recent alligators observed by Stoskopf et al. (2001). This implies that the alligator in this study was exposed to a lower range of $\delta^{18}O$ values from ingested drinking water during life than



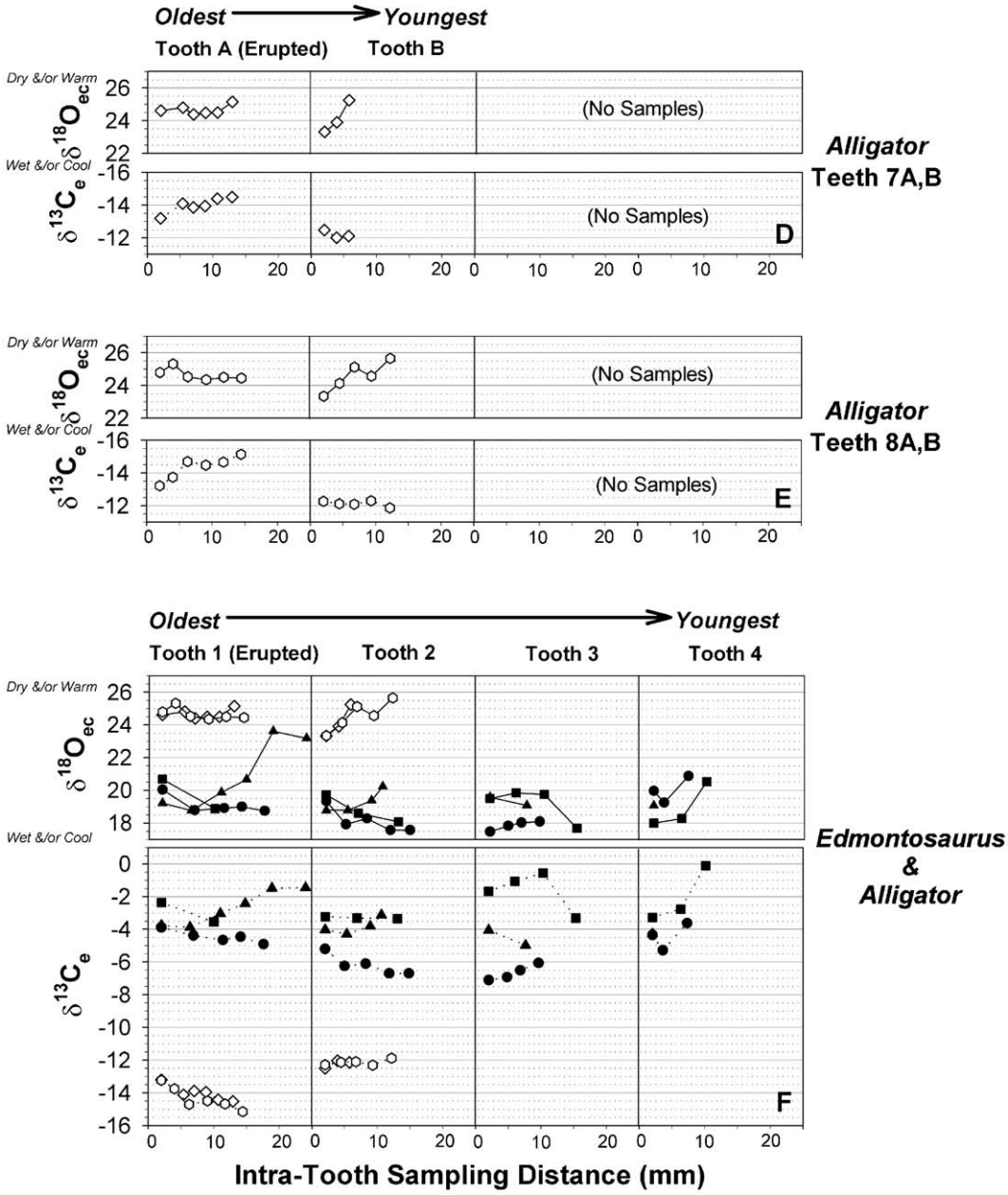


Fig. 4 (*continued*).

were the *Edmontosaurus* specimens, possibly because of reduced seasonality in its environment versus that of the dinosaurs (see Discussion).

Mean intra-tooth $\delta^{18}O_{ec}$ values show a decreasing (more negative) trend from oldest to youngest teeth in the juvenile (CC-MN-207) and sub-adult (CC-MN-1448) *Edmontosaurus* specimens, while in the oldest specimen (CC-MN-2070) the mean intra-tooth $\delta^{18}O_{ec}$ values decrease first, then increase. The adult specimen shows the greatest

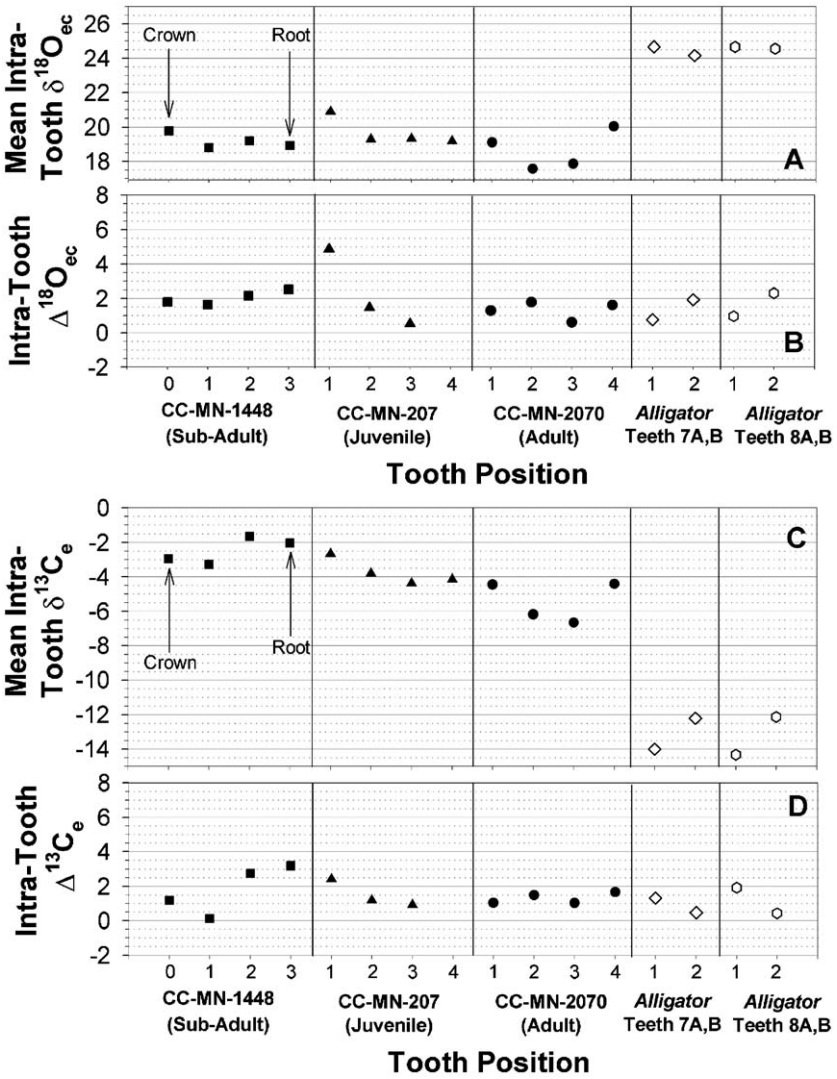


Fig. 5. Mean intra-tooth carbonate $\delta^{18}O_{ec}$ (A) and $\delta^{13}C_e$ (C), and intra-tooth $\Delta^{18}O_{ec}$ (B) and $\Delta^{13}C_e$ (D), for microsampled *Edmontosaurus* and modern *Alligator* enamel. $\Delta^{18}O_{ec}$ and $\Delta^{13}C$ are calculated as $\delta^{18}O_{high}-\delta^{18}O_{low}$ and $\delta^{13}C_{high}-\delta^{13}C_{low}$, respectively, for each tooth. Black triangles: juvenile *Edmontosaurus* (CC-MN-207); black squares: sub-adult Edmontosaurus (CC-MN-1448); black circles: adult *Edmontosaurus* (CC-MN-2070); open diamonds: *Alligator* teeth #7A,B; open hexagons: *Alligator* teeth #8A,B.

range in intra-tooth mean $\delta^{18}O_{ec}$ values (2.5 ‰; Fig. 5A).

Inter-tooth $\delta^{18}O_{ec}$ variability for all four *Alligator* teeth is 2.3 ‰ (measured values range from 23.3 ‰ to 25.7 ‰). This is significantly smaller than the total inter-tooth $\delta^{18}O_{ec}$ range of 6.1 ‰ for *Edmontosaurus* (measured values range from 17.5 ‰ to 23.6 ‰; see Appendix A). Mean *Alligator* $\Delta^{18}O_{ec}$ intra-tooth variability for all teeth sampled is 1.5 ‰, comparable to *Edmontosaurus* $\Delta^{18}O_{ec}$ (1.8 ‰). Likewise, the range of intra-tooth variability for *Alligator* (0.8 to 2.3 ‰) is similar to, although lower than, that of *Edmontosaurus* (0.5 ‰ to 4.8 ‰; Table 2, Fig. 5B).

4.2. Carbon isotopes from microsampled enamel

Edmontosaurus $\delta^{13}C_e$ values show the same pattern of gradual temporal increase or decrease seen in $\delta^{18}O_{ec}$,

with a significant positive co-variation between $\delta^{13}C_e$ and $\delta^{18}O_{ec}$ [$F(1,40)=321.59$, $P \ll 0.001$, $r^2=0.89$] using linear regression (Fig. 4A, B, C, F). Similar temporal $\delta^{13}C_e$ patterns are apparent in *Alligator* (Fig. 4B, C, F), although linear regression shows no significant co-variation between $\delta^{18}O_{ec}$ and $\delta^{13}C_e$ [$F(1,18)=0.11$, $P>0.001$, $r^2=0.01$].

The total range of $\delta^{13}C$ for all four *Alligator* teeth is 3.3 ‰ (measured values range from −11.9 ‰ to −15.1 ‰; Table 2 and Appendix A). This is smaller than the total range of 7.0 ‰for *Edmontosaurus* (measured values range from −0.1 ‰ to −7.1 ‰). Mean $\Delta^{13}C_e$ intra-tooth variability (for all teeth sampled) is slightly lower in the modern *Alligator* teeth (1.0 ‰) than in the *Edmontosaurus* (1.5 ‰). As with oxygen isotope values, the range of intra-tooth variability for *Alligator* (0.4 ‰ to 1.9 ‰) is similar to, although lower than, that of *Edmontosaurus* (0.1 ‰ to 3.2 ‰) (Table 2, Fig 5D).

4.3. Diagenetic tests: comparison of stable isotopes from microsampled enamel and bulk-sampled enamel, dentine, and bone from all specimens

While none is definitive, several methods exist for probing the degree of post-mortem isotopic alteration in fossil bioapatite. First, comparison of isotopes from modern and fossil analogs can establish "expected" isotope values in fossil specimens (Lee-Thorp and van der Merwe, 1987). Second, comparison of co-occurring $\delta^{18}O_c$ to $\delta^{18}O_p$, which should be in equilibrium in vivo but which undergo differential diagenetic alteration so that in unaltered isotopes $\delta^{18}O_p$ and $\delta^{18}O_c$ will vary co-linearly and have equal intra-tooth variance in homeotherms (animals with constant body temperature; Iacumin et al., 1996). Third, comparison of bone and dentine to enamel from the same individual, since bone and dentine are more readily altered than is enamel and should therefore show differences in mean isotope values and isotope variability between the different apatite types. Fourth, comparisons of bioapatite to sediment carbonates and organic carbon from the same stratigraphic level (Quade et al., 1992). Finally, use of SEM to identify original enamel crystallite structure (Kolodny et al., 1996).

Comparison of $\delta^{18}O_c$ versus $\delta^{13}C$ for *Edmontosaurus* bone, dentine and enamel, *Alligator* enamel, and modern *Rhea* and *Struthio* bone show significant differences (using Hotelling's T^2 test, a measure of variability within subgroups) among taxa and bioapatite type (i.e. "clouds" of data points categorized by both taxon and bioapatite type plot in statistically distinct areas of the graph; $P<0.0001$; Fig. 6). Mean $\delta^{18}O_{ec}$ values for *Edmontosaurus* enamel (19.2 ‰) are lower than those of dentine (22.9 ‰) and bone (23.1 ‰; Table 3). Mean $\delta^{18}O_c$ for ratite bone (23.2 ‰) is closer to *Edmontosaurus* dentine and bone values than to enamel values (Table 3).

Mean $\delta^{13}C$ values for *Edmontosaurus* enamel (−4.0 ‰) are also more negative than those of dentine (1.4 ‰) and bone (−2.2 ‰). Mean $\delta^{13}C$ for ratite bone (−9.9 ‰) is more negative than the *Edmontosaurus* enamel, dentine, and bone (Table 3). Mean $\delta^{13}C$ of replicate analyses from four different samples of organic carbon from bonebed sediments ($\delta^{13}C_{oc}$) is −26.02 ‰, an average value for modern C3 plants.

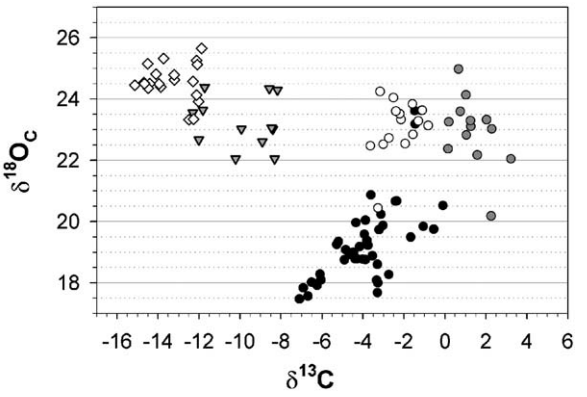


Fig. 6. $\delta^{18}O_c$ versus $\delta^{13}C$ for enamel, dentine, and/or bone from *Edmontosaurus*, *Alligator*, and modern ratites (*Struthio* and *Rhea*). Open diamonds: modern *Alligator* enamel; gray triangles: modern ratite bone; black circles: *Edmontosaurus* enamel; gray circles: *Edmontosaurus* dentine; open circles: *Edmontosaurus* bone (cancellous and cortical). Note that *Edmontosaurus* dentine and bone have significantly more positive $\delta^{18}O_c$ than does *Edmontosaurus* enamel, indicative of greater alteration in the dentine and bone during low temperature postmortem alteration by diagenetic minerals versus higher temperatures during in vivo biomineral formation (P. Koch, 2002, personal communication). The observed more positive $\delta^{18}O_c$ values in modern *Alligator* enamel versus *Edmontosaurus* enamel are also expected if enamel is relatively unaltered due to differences in thermophysiology and latitudinal and ambient temperature variation between habitats (P. Koch, 2002, personal communication).

Table 3
Summary of mean carbonate oxygen ($\delta^{18}O_c$) and carbon ($\delta^{13}C$) for bulk and microsampled bone, dentine, and enamel from *Edmontosaurus* and modern *Alligator*, *Struthio*, and *Rhea*

Specimen	No. of samples	Mean $\delta^{18}O_C$ (‰)	S.D.	Total range	Mean $\delta^{13}C$ (‰)	S.D.	Total range
Edmontosaurus							
Enamel	42	19.2	1.3	6.1	−4.0	1.7	7.0
Dentine	13	22.9	1.1	4.8	1.4	0.9	3.1
Bone[a]	16	23.1	0.9	3.8	−2.2	0.9	2.8
Alligator							
Enamel	20	24.6	0.6	2.3	−13.4	1.1	3.3
Ratite							
Bone	12	23.2	0.8	2.3	−9.9	1.7	4.1

External precision for carbonate analyses is accurate to hundredths; however, for consistency with reported phosphate oxygen values (see Appendix A), all isotope values are reported to tenths.
[a] Cortical and cancellous.

Comparison of $\delta^{18}O_p$ to $\delta^{18}O_c$ for *Edmontosaurus* enamel, dentine, and bone and modern ratite bone shows that none of the bioapatite types plot directly on the theoretical $\delta^{18}O_p$–$\delta^{18}O_c$ line (Longinelli and Nuti, 1973; Kolodny et al., 1983; Iacumin et al., 1996; Fig. 7; see Discussion).

Box plots of $\delta^{18}O_p$ and $\delta^{18}O_c$ for *Edmontosaurus* enamel, dentine, and bone and modern ratite bone show that $\delta^{18}O_c$ is more variable in the 25th to 75th percentile data spreads (i.e. within boxes) for all bioapatite types—including modern ratite bone—than is $\delta^{18}O_p$ (Fig. 8). Total variability ($\Delta^{18}O_c$, including outliers) is also higher than $\Delta^{18}O_p$ for fossil bioapatite types (enamel, dentine, and cortical bone), with one exception: cancellous dinosaur bone (Fig. 8). $\Delta^{18}O_p$ and $\Delta^{18}O_c$ are equal in ratite bone (2.3 ‰). Results of all isotopic analyses (microsampled teeth and bulk sampled bone, dentine, and teeth, for *Edmontosaurus*, *Alligator*, *Struthio*, and *Rhea*) are presented in the Appendix A.

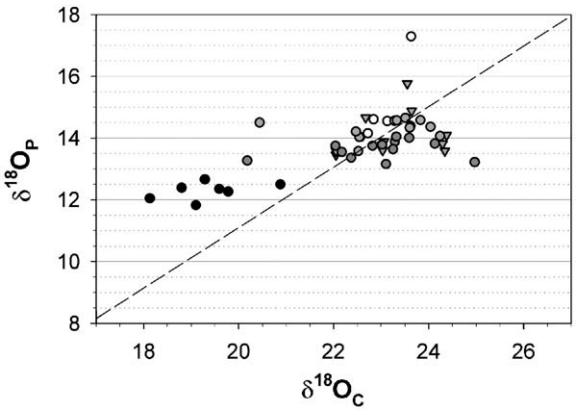


Fig. 7. $\delta^{18}O_p$ versus $\delta^{18}O_c$ for *Edmontosaurus* enamel, dentine, and bone, and modern ratite bone. Dashed line represents expected in vivo equilibrium between $\delta^{18}O_p$ and $\delta^{18}O_c$ in modern mammals ($y = 0.98 \times - 8.5$) ($r^2 = 0.98$) (Iacumin et al., 1996). Gray triangles: modern ratite bone; black circles: *Edmontosaurus* enamel; dark gray circles: *Edmontosaurus* dentine; light gray circles: *Edmontosaurus* bone (cortical); open circles: *Edmontosaurus* bone (cancellous). Note that the distribution of data points does not match the predicted mammalian line, even in modern (i.e. unaltered) ratite. Thus, archosaurs (which include birds, non-avian dinosaurs, and crocodilians) may have a different linear relationship between $\delta^{18}O_p$ and $\delta^{18}O_c$ than do mammals.

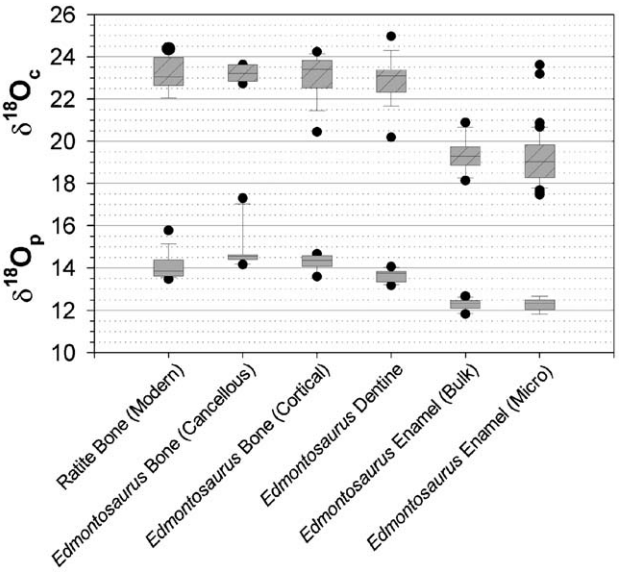


Fig. 8. Comparison of variance in $\delta^{18}O_p$ and $\delta^{18}O_c$ in *Edmontosaurus* and modern ratites. Boxes are bounded by the 25th and 75th percentiles and bisected by the 50th percentile. The lines are drawn out to the 10th and 90th percentiles; points outside of these limits represent outliers. Assuming that $\delta^{18}O_p$ is unaltered (possibly an unwarranted assumption), greater variability in *Edmontosaurus* $\delta^{18}O_c$ may represent diagenetic alteration in this component. However, greater variability in $\delta^{18}O_c$ than $\delta^{18}O_p$ is also observed in modern ratite bone, which is known to be unaltered. Small sample numbers for *Edmontosaurus* enamel $\delta^{18}O_p$ ($n = 7$) and *Edmontosaurus* bone $\delta^{18}O_p$ ($n = 4$) may also affect the observed variability in these tissues (see Appendix A).

5. Discussion

5.1. Evaluating the possibility of diagenetic alteration

Evaluation of diagenesis in fossil bioapatites is best accomplished by utilizing several types of analyses, each of which will independently provide evidence for or against alteration of original isotope values (Rink and Schwarz, 1995; Iacumin et al., 1996; Kolodny et al., 1996; Barrick, 1998; Kohn et al., 1999; Sharp et al., 2000). No single test will conclusively indicate pristine preservation (Nelson et al., 1986). Support for at least partial diagenetic alteration of some of the bioapatites in this study (especially bone and dentine) exists, but is contrasted with other evidence that points to at least a partial signal being retained by enamel.

The *Edmontosaurus* specimens obtained for this analysis were all deposited within the same bonebed, ensuring that all three individuals were alive at approximately the same time, likely obtained food and water from similar sources, died at relatively the same time and in the same place, and were subjected to similar postmortem diagenetic processes. This alleviates potential problems in interpretation of $\delta^{18}O$ and $\delta^{13}C$ values due to variation in latitude, precipitation, humidity, temperature, age, or diet (assuming little ontogenetic dietary change; Dansgaard, 1964; Kolodny et al., 1996; Barrick, 1998; Koch, 1998; Fig. 1A).

SEM analysis of *Edmontosaurus* enamel shows that the micro-scale crystalline structure of the enamel is preserved (Fig. 3C), a prerequisite to preservation of original isotope values (Kolodny et al., 1996). The presence of wavy enamel is readily evident in SEM micrographs of the *Edmontosaurus* specimens used in this study (Fig. 3A). Mean thickness of *Edmontosaurus* enamel is 181 μm ($\sigma = 36.8$, $n = 14$). Mean thickness of *Alligator* enamel is 267 μm ($\sigma = 17.2$, $n = 7$; this study; Fig. 3A, B).

The presence of seasonal patterns in the modern *Alligator* enamel and their similarity to seasonal patterns identified in modern mammals (Koch et al., 1989, 1998; Fricke and O'Neil, 1996; Stuart-Williams and Schwarz, 1997; Fricke et al., 1998a; Kohn et al., 1998; Sharp and Cerling, 1998; Feranec and MacFadden, 2000; Wurster and Patterson, 2001; Passey and Cerling, 2002) strongly suggests that similar patterns found in *Edmontosaurus* enamel are seasonal in nature (Fig. 4F). The presence of these seasonal signals in microsampled *Edmontosaurus* enamel can be interpreted in two ways (Fig. 4A, B, C). First, it suggests that the $\delta^{18}O_{ec}$ values are unaltered. However, diagenesis tends to homogenize seasonal signals when isotope values are "re-set" to those of the surrounding sediments and local meteoric waters that percolate through the sediments (Quade et al., 1992). Thus, a second possible interpretation is that, while the *absolute* $\delta^{18}O_{ec}$ values might be altered, the *pattern* of seasonal isotope variation has been retained (although it may be dampened due to diagenetic alteration). Unfortunately, sediments from the *Edmontosaurus* bonebed lack carbonates, and cannot therefore be compared to those of enamel and bone as a further test of diagenesis.

Because of their ectothermy and smaller body masses, modern alligators from Louisiana (latitude ~ 30 °N) likely mineralize bioapatite at lower body temperatures (Kirk and Hogben, 1946; Hotton, 1980; Coulson et al., 1989) and higher ambient temperatures than did Maastrichtian hadrosaurs from South Dakota (paleolatitude ~ 43° N, compared to ~ 46° N for the site today; Smith and Briden, 1977). If this is the case, then diagenetically unaltered *Edmontosaurus* bioapatite should display less positive $\delta^{18}O_{ec}$ values than does *Alligator* bioapatite. Because the *Edmontosaurus* specimens do follow this predicted pattern, we interpret it as evidence that the *Edmontosaurus* enamel retains the original isotopic signature (Table 3; Fig. 6).

Results of $\delta^{18}O_c$ versus $\delta^{13}C$ for dinosaur bioapatites also suggest that enamel samples may retain their original values, or at least do not appear to be as altered as the bone and dentine (Fig. 6). $\delta^{18}O_c$ values for cancellous and cortical bone and dentine are significantly more positive than those for enamel—the result predicted if the enamel mineralized in vivo at higher temperatures of formation than did diagenetic minerals preferentially affecting the bone and dentine (Fig. 6). This is suggestive of more faithful preservation of $\delta^{18}O$ values in enamel than in bone and dentine in the *Edmontosaurus* specimens.

Evidence of at least minimal alteration in the *Edmontosaurus* bioapatite is indicated by comparing the range of $\delta^{18}O_p$ and $\delta^{18}O_c$, where $\delta^{18}O_c$ values show higher variability than for $\delta^{18}O_p$ samples from the same specimens (Fig. 8). Because bioapatite phosphate oxygen is considered to be more resistant to

diagenesis than is carbonate oxygen, it is commonly used as a proxy for "expected" $\delta^{18}O_c$ ranges, and higher variability in $\delta^{18}O_c$ values (than in $\delta^{18}O_p$) are therefore inferred to be diagenetic (Showers et al., 2002). This approach assumes that the $\delta^{18}O_p$ is itself unaltered—an assumption that is not necessarily robust, but is also difficult to test using current methods (Kolodny et al., 1996; Longinelli, 1996; Goodwin et al., 2002). Greater variability in $\delta^{18}O_p$ versus $\delta^{18}O_c$ may also be related to the analytical precision for these two components, which is five times greater in $\delta^{18}O_c$ than in $\delta^{18}O_p$, so variability in $\delta^{18}O_p$ values might be exaggerated relative to $\delta^{18}O_c$ analyzed from the same samples.

In mammals, $\delta^{18}O_p$ and $\delta^{18}O_c$ are linearly correlated because phosphate and carbonate are mineralized in equilibrium from the same oxygen source (body water) at the same temperature ($\sim$ 37 °C) according to the equation:

$$\delta^{18}O_p = 0.98\delta^{18}O_c - 8.5 \quad (1)$$

(Iacumin et al., 1996). Comparison of $\delta^{18}O_p$ to $\delta^{18}O_c$ for *Edmontosaurus* enamel, dentine, and bone shows that none of the fossil bioapatite types plot directly on the theoretical mammalian $\delta^{18}O_p$–$\delta^{18}O_c$ line (Fig. 7). Surprisingly, modern ratite bone (known to be isotopically unaltered) also shows large variation about the expected linear correlation (Fig. 7). Of all four bioapatite types (cortical and cancellous bone, dentine, and enamel), the *Edmontosaurus* enamel plots farthest from the line of Eq. (1), with the exception of several outliers. This is opposite to the predicted pattern if (1) bone and dentine are more readily altered than enamel and (2) dinosaurs follow the predicted mammalian pattern of a linear relationship according to Eq. (1). Because neither the unaltered modern ratite bone nor the *Edmontosaurus* specimens plot on the predicted line, this linear $\delta^{18}O_p$–$\delta^{18}O_c$ relationship may not be as closely correlated for archosaurs (which include birds, non-avian dinosaurs, and crocodilians) due to physiological effects as it is in mammals. Conversely, if archosaur $\delta^{18}O_p$–$\delta^{18}O_c$ *is* linearly correlated, the line may have a different slope than Eq. (1), which is empirically derived from mammalian isotope data. To date this hypothesis has not been tested. It should be noted that small sample sizes in this study further complicate interpretation of this test. As previously mentioned, no data exist to determine whether or not dinosaurs exhibit the same relationship between $\delta^{18}O_p$ and $\delta^{18}O_c$ as do mammals, or whether they are offset from the mammalian model due to physiological differences. We are currently investigating this potentially valuable possibility.

Diagenetic alteration of isotopes in bioapatite carbon is difficult to recognize. Based on groundwater exchange experiments on modern and fossil organisms, evidence indicates that unlike inorganic carbonates, carbon in bioapatite is relatively resistant to diagenesis (Krueger, 1991). This conclusion is supported by an analysis of the structural carbonate in fossil teeth from Badlands National Monument in South Dakota, in which $\delta^{13}C_{ec}$ values appear to have been preserved since the Early Oligocene (Wang and Cerling, 1994).

Mean $\delta^{13}C$ values in this study are more positive in the bone and (especially) dentine than in enamel (Fig. 6). This suggests that bone and dentine are preferentially altered, possibly by marginal-marine carbonates ($\delta^{13}C$ $\sim$ 1–2‰) due to the proximity of the bonebed to the Western Cretaceous Interior Seaway, rather than representing a terrestrial dietary signal (Koch et al., 1992). Significant co-variation of $\delta^{13}C_e$ and seasonal patterns in $\delta^{18}O_{ec}$ can potentially be used as an indicator of carbon isotope preservation (Fig. 4). If corresponding to seasonal variation in dietary plant intake, co-variation is indicative of an original isotopic signal. However, it is also possible that co-variation between $\delta^{13}C_e$ and $\delta^{18}O_{ec}$ is the result of microscale diagenetic alteration along enamel growth lines (P. Koch, 2002, personal communication). Because hadrosaurids lack visible Striae of Retzius (enamel growth lines; Sander, 2000), however, it is likely that co-variation exists due to seasonal variation in plant intake that results in small variations in $\delta^{13}C_e$. We interpret the depleted $\delta^{13}C_e$ values relative to dentine and bone, along with co-variation of $\delta^{13}C_e$ and $\delta^{18}O_{ec}$ in *Edmontosaurus* and to a lesser degree in modern *Alligator*, as evidence of preferential preservation of *Edmontosaurus* $\delta^{13}C_e$ relative to bone and dentine $\delta^{13}C_b$.

The presence of an average C3 plant isotopic signal (mean = – 26.0‰) in $\delta^{13}C_{oc}$ from bonebed sediments is also significant for evaluation of $\delta^{13}Ce$ diagenesis. Assuming that organic material is isotopically unaltered, autochthonous, and that it comprised the same

plant material ingested by *Edmontosaurus* (assumptions that are admittedly difficult to test currently), we infer that the observed $\delta^{13}C_{oc}$ is either indicative of diagenetic alteration in $\delta^{13}C_e$ (which is much more enriched than predicted for a C3 herbivore), or that *Edmontosaurus* exhibited a different $\delta^{13}C$ fractionation factor of $\sim 13‰$ versus modern mammals (see Section 5.3).

5.2. Carbonate oxygen isotopes

Seasonal isotopic signals have been reported from mammalian tooth enamel and fish otoliths (Koch et al., 1989, 1998; Fricke and O'Neil, 1996; Stuart-Williams and Schwarz, 1997; Fricke et al., 1998a; Kohn et al., 1998; Sharp and Cerling, 1998; Feranec and MacFadden, 2000; Wurster and Patterson, 2001; Passey and Cerling, 2002). However, studies of this type are rare for dinosaurs (Patchus et al., 2001; Thomas and Carlson, 2001). Our analysis represents one of the first micro-scale isotopic analyses of a monospecific dinosaur through ontogeny. The presence of what we interpret to be partial seasonal signals in *Edmontosaurus* dental enamel has broad implications for hadrosaur ontogeny, physiology, and ecology.

Plots of $\delta^{18}O_{ec}$ versus relative time (sampling distance) for microsampled *Edmontosaurus* specimens are interpreted as partial seasonal signals based on similarities of these patterns to seasonal signals detected in studies of modern tooth enamel (Dansgaard, 1964; Fricke and O'Neil, 1996; Stuart-Williams and Schwarz, 1997; Fricke et al., 1998a; Kohn et al., 1998; Passey and Cerling, 2002; Fig. 4). Assuming the retention of a primary seasonal signal, we can attempt to reconstruct the season of mineralization for *Edmontosaurus*. In both the sub-adult (CC-MN-1448) and adult (CC-MN-2070), tooth #1 appears to have been mineralized from the dry and/or warm to the wet and/or cool seasons, while in tooth #1 of the juvenile (CC-MN-207), mineralization appears to have occurred primarily from wet and/or cool season to the warm and/or dry—opposite that of the larger individuals. It has been shown in previous analyses of modern tooth enamel that $\delta^{18}O_{ec}$ values are a reflection of season of deposition, because $\delta^{18}O$ of water ingested by organisms fluctuates during warm/dry and cool/wet seasons due to differential evaporation (Fricke and O'Neil, 1996; Stuart-Williams and Schwarz, 1997; Fricke et al., 1998a; Kohn et al., 1998; Passey and Cerling, 2002). Because dinosaurs shed and replace their teeth repeatedly throughout life (polyphyodonty; Edmund, 1960), this pattern of inter-jaw seasonal variability is not unexpected if intra-tooth season of mineralization is also variable. Of the 12 teeth sampled from all three *Edmontosaurus* specimens, five appear to have been mineralized from a warm/dry to cool/wet season; four from cool/wet to warm/dry, and three were difficult to assess due to the small number of samples available per tooth (Fig. 4A, B, C). Based on these results, we hypothesize that *Edmontosaurus* mineralized teeth year-round, instead of preferentially during specific seasons. This interpretation assumes a homeothermic metabolism for these animals, which is in keeping with their large body size, highly vascularized bone, and proposed fast juvenile growth rates (O'Connor and Dodson, 1999; Horner et al., 2000; Erickson, 2001; Padian et al., 2001).

Assuming 6-month cold/wet and 6-month warm/dry seasonality, the presence of partial (instead of complete) seasonal signals in all sampled *Edmontosaurus* teeth indicates that this species mineralized enamel in < 0.65 year, with slightly shorter mean tooth formation rates in sub-adult and juvenile hadrosaurs than in adults (with the exception of tooth #1 in specimen CC-MN-207; Fig. 4F). This pattern is comparable to Erickson's (1996b) estimate (using counts of lines of von Ebner in dentine) of tooth mineralization times of 225 days (~ 0.62 year) in *Edmontosaurus* juveniles. However, estimates of adult *Edmontosaurus* tooth formation time differ between the two studies. We calculate a tooth formation time of ~ 0.5 "cycles," or ~ 183 days, while Erickson (1996b) calculates 339 days for an adult *Edmontosaurus*. Other teeth in our study are similarly estimated to have formed in shorter time periods than Erickson's (1996b) estimates. These discrepancies between tooth formation times using $\delta^{18}O_{ec}$ seasonal signals versus counts of growth lines in dentine could be due to (1) longer times of dentine formation than enamel formation (i.e. enamel stops mineralizing before dentine; G. Erickson, 2002, personal communication); (2) the limited number of microsamples obtained (a maximum of 6 per tooth), which could time-average finer-scale variations preserved in ~ 15 μm wide lines of von Ebner (Erickson, 1996b), (3) microsampled measurements of less than the entire enamel length due to incomplete preservation in the tooth specimen,

or (4) seasonality at this locality was other than 6 months cool/wet and 6 months warm/dry. Regardless, values obtained for enamel mineralization rates in this study and dentine mineralization rates of Erickson (1996b) are broadly in agreement, despite the different methods used to calculate the timing of tooth growth.

Using the most complete seasonal signal measured we can calculate growth rates using the method of (Fricke and O'Neil, 1996). The enamel measured in the juvenile (CC-MN-207, tooth #1) represents ~0.65 seasonal cycles and 25.5 mm of growth up the length of the tooth; this corresponds to 3.2 mm/month growth or ~38 mm/year. This compares to the rate of 40 mm/year for a fossil bison and 21 mm/year for a modern sheep calculated by (Fricke and O'Neil, 1996). Growth rates calculated in this manner are simply an estimate of the length of enamel mineralized along the tooth (measured from crown to root) during a given time period; they do not take into account differences in enamel thickness between different species. Assuming that the above estimates are reasonable, this implies that mammals may mineralize a much larger volume of enamel over the same time period than did *Edmontosaurus*, since mammalian enamel is much thicker (e.g. 2.5 mm in humans; Scott and Symons, 1971) than dinosaurian (Sander, 2000).

Using the same method to calculate mineralization rates for the modern *Alligator* specimen (and again assuming a 6-month cold/wet and 6-month warm/dry seasonality), we estimate that the measured seasonal cycles (Fig. 4D, E) represent ~0.3 year (based on mean Alligator tooth replacement rates of ~120 days, Erickson, 1996a). The enamel measured for tooth 7A is 12.07 mm; at 0.3 cycles this represents mineralization rates of ~3 mm/month, or 36 mm/year. This is very close to the estimated mineralization rate of ~38 mm/year for *Edmontosaurus*, implying that modern alligators and *Edmontosaurus* (which have comparable enamel thickness) were apparently mineralizing enamel at approximately similar rates.

Explanations other than seasonality are possible but unlikely to explain the $\delta^{18}O_{ec}$ variability seen in *Edmontosaurus*. Because $\delta^{18}O_{ec}$ is largely dependent on the isotopic value of ingested drinking water, enriched (e.g. evaporated pools) or depleted (e.g. freshwater lakes and streams) sources of water affect $\delta^{18}O$ in mineralized tissues; the same processes can also affect $\delta^{18}O$ in plants (which obtain water from a variety of sources) ingested by dinosaurs and subsequently incorporated into enamel. However, because enriched/depleted $\delta^{18}O$ sources are probably ultimately seasonally driven (because enrichment and depletion in $\delta^{18}O$ are associated with freshwater influx and evaporation rates, respectively), it is likely that the $\delta^{18}O_{ec}$ patterns observed ultimately do have a seasonal source, and that (assuming a lack of diagenesis) the variations seen in the *Edmontosaurus* dental enamel are in fact seasonally derived.

Another possible explanation for $\delta^{18}O_{ec}$ variability seen in the *Edmontosaurus* teeth is migration, which would expose the animals to a wide range of $\delta^{18}O$ values from latitudinal, humidity, precipitation, and temperature variations. Indirect evidence for migration in hadrosaurs along the western shore of the Western Interior Cretaceous Seaway exists (Hotton, 1980; Horner and Gorman, 1988; Currie, 1989), and it is not difficult to imagine that they may have been behaving in a similar manner along the eastern shoreline of the seaway, where *Edmontosaurus* specimens used in this study were living. However, as most animals migrate to stay within certain temperature ranges or food sources, seasonal variation of $\delta^{18}O_{ec}$ would most likely be homogenized if these animals were migrating (P. Koch, 2002, personal communication). Thus, it seems likely that the seasonal signals observed in $\delta^{18}O_{ec}$ are the result of localized seasonal variation in $\delta^{18}O$ rather than migration.

5.3. Carbon isotopes

$\delta^{13}C$ in biominerals is correlated with dietary preferences in mammals and other vertebrates (reviewed in Barrick, 1998; Koch, 1998). Few attempts have been made to correlate dinosaur $\delta^{13}C$ values to dietary resources, and these have been limited to analyses of preserved organic material in dinosaur teeth and bones (Bocherens et al., 1988, 1991; Ostrom et al., 1990). To our knowledge, this study represents a first, albeit speculative, attempt to glean dietary information from carbon isotope analysis of dinosaurian enamel.

Carbon isotopes are differentially fractionated in plants depending on whether they use C3 or C4 photosynthetic pathways (Smith and Epstein, 1971). C3 plants are adapted to temperate conditions and include most trees, shrubs, ferns, and cool-season grasses; C4 plants are adapted to higher temperatures

and drier conditions and include warm-season grasses, some sedges, and herbs (Koch, 1998). Isotopic differences between C3 and C4 plants can be used to identify food sources in herbivores and the evolutionary timing and distribution of plants (Quade et al., 1992, 1995; Cerling and Quade, 1993; Morgan et al., 1994; Quade and Cerling, 1995; Cerling et al., 1998). C3 photosynthesis results in an atmospheric CO_2-to-plant tissue fractionation of ~ -19.5‰, and $\delta^{13}C_{atm} \cong -6.5$‰; therefore C3 plant tissues have $\delta^{13}C_p \cong -26$‰. C4 photosynthesis results in fractionation of ~ -5.5‰, and resulting C4 plant tissues have $\delta^{13}C_p \cong -12$‰. Mammalian herbivores ingesting these plants further fractionate by ~ 13‰; therefore mammalian bioapatites have mean $\delta^{13}C$ values of ~ -13‰ (for C3 browsers) and $\sim +1$‰ (for C4 grazers; Fig. 1B). These values can vary somewhat based on $\delta^{13}C_{atm}$ (which may change over geological time), water or salinity stress, or by taxon. Thus, $\delta^{13}C$ from mammalian bioapatite can range from -9‰ to -22‰ for C3 browsers and -6‰ to $+4$‰ for C4 grazers (Koch, 1998).

It is presumed that *Edmontosaurus* was primarily a C3-plant feeder because isotopic evidence for the spread of C4 plants does not appear before ~ 7 Ma, during the late Miocene (Quade et al., 1992; Cerling and Quade, 1993; MacFadden, 1994; MacFadden and Cerling, 1996; Koch, 1998). However, measured carbon isotope values for the *Edmontosaurus* specimens presented here are more positive than expected for an herbivore presumably feeding on C3 plants: mean $\delta^{13}C_e$ for all specimens is -4‰ (total range -0.1‰ to -7.1‰; Table 3). Such values in modern mammals would be indicative of a mixed C3/C4 to 100% C4 diet (Koch, 1998). Given the apparent lack of C4 plants during the Late Cretaceous, however, other mechanisms must be called upon to explain the enriched $\delta^{13}C_e$ values. Several possible scenarios exist. First, the values may represent an original biogenic signal that is shifted due to environmental factors such as the $\delta^{13}C_{atm}$, $\delta^{13}C_p$, or proximity to the Cretaceous Western Interior Seaway. Second, they could represent an original biogenic signal that is shifted due to fractionation differences between mammals and dinosaurs. Third, the enriched $\delta^{13}C_e$ values may result from a combination of the above factors. Fourth, *Edmontosaurus* may have consumed primarily CAM plants (a third photosynthetic pathway whose $\delta^{13}C_p$ can overlap those of C3 and C4 plants; Bender et al., 1973). Fifth, contrary to all existing evidence, C4 plants may have been present in the Late Cretaceous and constituted a portion of *Edmontosaurus*' diet. Finally, the enriched values may be the result of diagenetic alteration.

Assuming that the $\delta^{13}C_e$ values are original and not diagenetic (see Section 5.1), more enriched $\delta^{13}C_{atm}$ (~ 1.5–2‰ during the Late Cretaceous; Ekart et al., 1999; Arens and Jahren, 2000), could have caused a corresponding positive shift in $\delta^{13}C_p$ of Cretaceous plants (Marino and McElroy, 1991; Bocherens et al., 1993; Elliott, 1999). Herbivorous dinosaurs feeding on these enriched plants would consequently be equally (1.5–2‰) enriched in $\delta^{13}C_{ec}$. In addition to isotopically enriched $\delta^{13}C_{atm}$, atmospheric pCO_2 levels were also likely high in the Late Cretaceous (Lasaga et al., 1985; Berner, 1994; Ekart et al., 1999; Retallack, 2001; Royer et al., 2001). Because $\delta^{13}C_p$ is directly correlated with $\delta^{13}C_{atm}$ rather than with pCO_2 levels, however, it is unlikely that elevated pCO_2 had a direct effect on $\delta^{13}C_e$ (Arens et al., 2000). Also, the presence of an average C3 signal in bonebed $\delta^{13}C_{oc}$ indicates that enriched $\delta^{13}C_{atm}$ is not the most likely explanation of enriched $\delta^{13}C$ in *Edmontosaurus*.

Plant-specific dietary factors could also account for some of the measured $\delta^{13}C_e$ enrichment. Palynological analysis shows that *Edmontosaurus* bonebed pollen is composed of $\sim 46\%$ gymnosperms (primarily cypress), 43% angiosperms (primarily broad-leafed trees), and $\sim 11\%$ ferns (R. Nellermoe, 2002, unpublished data). Previous cranial and dental studies indicate that hadrosaurs could masticate their food and likely fed primarily on high-fiber diets such as gymnosperms and ferns (Kräusel, 1922; Weishampel, 1984; Farlow, 1987; Norman and Weishampel, 1987; Chin and Gill, 1996) and angiosperms (Weishampel and Norman, 1989). Although gymnosperms are C3 plants, they are typically enriched, on average, by 1.1‰ from mean C3 values, and can be up to 2.5‰ enriched in certain species with scale leaves (including cypress) (Marshall and Zhang, 1994). *Edmontosaurus* feeding primarily on gymnosperms (and particularly cypress) would therefore be expected to have similarly enriched $\delta^{13}C_e$. The presence of an average C3 signal in bonebed $\delta^{13}C_{oc}$ may indicate that these *Edmontosaurus* specimens were not feeding from the same plants from which the bonebed organics originated, either because

the organics are allochthonous, or because *Edmontosaurus* was feeding remotely.

Proximity to the Cretaceous Western Interior Seaway and its effects on local plants could also have played a role in enriched $\delta^{13}C_e$ in these *Edmontosaurus*. The specimens are interpreted as having been buried in a transitional coastal swamp to fluvial-dominated distributary on the eastern shore of the inland sea (R. Nellermoe, personal communication). It has been shown that halophytes (plants adapted to high salinity environments) respond to osmotic stress (i.e. high salinity) by increasing isotopic fractionation (i.e. preferentially retaining ^{13}C over ^{12}C during photosynthesis), with resulting $\delta^{13}C_p$ becoming more positive—by up to +10.8‰ in one extreme case (Guy et al., 1980; Farquhar et al., 1982). C3 salt marsh plants (e.g. saltgrass) also have relatively enriched $\delta^{13}C_p$, ranging from −23‰ to −26‰ (Smith and Epstein, 1970; Haines, 1976). Due to their proximity to the Western Interior Seaway coastal environment, it is quite possible that the *Edmontosaurus* specimens fed at least occasionally on osmotically stressed plants and thus would be expected to have enriched $\delta^{13}C_p$.

The previous three interpretations for enriched $\delta^{13}C_e$ in *Edmontosaurus* tooth enamel are not mutually exclusive. For example, if we assume that (1) Late Cretaceous $\delta^{13}C_{atm}$ was 1.5 to 2‰ more enriched than today; (2) that dietary $\delta^{13}C_p$ was close to the average of gymnosperms, which is ~1.1‰ to 2‰ heavier than most C3 plants; and (3) that the diet of *Edmontosaurus* included some plants that were osmotically stressed (causing ~2% to 3‰ enrichment in $\delta^{13}C_p$), we predict that $\delta^{13}C_e$ will be enriched by 4.5% to 7‰ from expected C3 bioapatite values (−9‰ to −22‰, assuming "mammalian" $\delta^{13}C_{diet}-\delta^{13}C_e$). In other words, we predict that the widest possible observed $\delta^{13}C$ range for C3 plant ingesting *Edmontosaurus* should be −2‰ to −17.5‰. The mean $\delta^{13}C_e$ for all *Edmontosaurus* specimens (−4.0‰) falls within this estimate, as do most values in the total $\delta^{13}C_e$ range (−0.1‰ to −7.1‰), making it at least possible that the enriched $\delta^{13}C_e$ observed in the *Edmontosaurus* specimens are environmentally induced, rather than diagenetic.

Another factor contributing to the enriched $\delta^{13}C_e$ in *Edmontosaurus* could be taxon-specific physiological mechanisms. Current models of biological fractionation between $\delta^{13}C_p$ and $\delta^{13}C_e$ are well constrained based on analyses of modern mammalian herbivore biominerals, and consequently fossil mammalian C3 and C4 feeders can be readily identified using $\delta^{13}C$ analysis (e.g. DeNiro and Epstein, 1978; Lee-Thorp and van der Merwe, 1987; Bocherens et al., 1996; Koch, 1998). Unfortunately, comparisons of this type are not possible for fossil specimens that lack a direct modern analog (e.g. *Edmontosaurus*), and consequently fractionation factors for mammals are used as a "benchmark" for estimating dinosaur fractionation factors. However, support for use of a mammalian fractionation model for dinosaurs is lacking. Comparisons to the closest extant relatives of *Edmontosaurus* are likely more appropriate than the mammalian analog, but data on $\delta^{13}C$ of bioapatite from extant archosaurs (the group encompassing dinosaurs, birds, and crocodilians) is rare. It is known that that herbivorous birds feeding on C3 and C4 plants have organic tissue (e.g. bone collagen and muscle) $\delta^{13}C$ values similar to that of mammals (reviewed in Kelly, 2000). Published data on alligator or crocodile bioapatite $\delta^{13}C$ is even more scarce than that for birds. Our data show *A. mississippiensis* to have mean $\delta^{13}C_e$ of −13.4 ±1.1‰ (Table 2). Previous studies have established that carnivore tissue is enriched ~1‰ to 2‰ from $\delta^{13}C$ of its prey (Kelly, 2000). Assuming fractionation equivalent to mammals, this suggests that these specimens were consuming prey with $\delta^{13}C$ values of ~−12.4‰ to −11.4‰, which is on the "enriched ^{13}C" end of C3 herbivores (−9‰ to −22‰; Koch, 1998). While it seems likely that extant birds and crocodilians have a $\delta^{13}C_p-\delta^{13}C_{bioapatite}$ fractionation similar to mammals, it is unclear from existing data if the fractionation is identical. It should also be noted that, while birds and crocodilians are most closely related to dinosaurs, little doubt remains that fundamental physiological differences exist between dinosaurs and their extant relatives—just as fundamental differences exist between avian and crocodilian physiologies. Hence, the question of fractionation between $\delta^{13}C_p-\delta^{13}C_{bioapatite}$ in dinosaurs remains equivocal due to (1) a lack of direct modern analogs for comparison, and (2) potentially significant physiological differences between hadrosaurs and their closest living relatives (birds and crocodiles), and mammals.

Finally, it is possible that the enriched $\delta^{13}C_e$ values are original and unaltered and that $\delta^{13}C_p-\delta^{13}C_e$ fractionation in *Edmontosaurus* (and presumably other

dinosaurs) is similar to mammals. If correct, then *Edmontosaurus* $\delta^{13}C$ values are direct evidence of either C4 plants in the Late Cretaceous, or its feeding on plants possessing $\delta^{13}C_p$ values that overlap C4 values (e.g. CAM plants, which range from -11‰ to -30‰; Bender et al., 1973). Both scenarios are unlikely, however. Pollen analyses of the *Edmontosaurus* bonebed show no evidence of CAM plants, and evidence for C4 plants prior to the Miocene is lacking. It has been suggested that the evolution of C4 plants was associated with low pCO_2 levels (Ehleringer et al., 1991, 1997), so that high pCO_2 levels inferred for the Late Cretaceous make it unlikely that C4 plants played a large (if any) part in the diet of *Edmontosaurus* (Lasaga et al., 1985; Berner, 1994; Ekart et al., 1999; Retallack, 2001; Royer et al., 2001).

In contrast to environmental effects that may cause isotopic enrichment, humidity can cause a relative depletion of $\delta^{13}C_p$. This could potentially mitigate some of the previously mentioned factors that cause more positive than expected $\delta^{13}C_e$ in *Edmontosaurus*. While effects of humidity are difficult to evaluate from paleoclimate records, it has been shown that experimentally controlled humidity levels can cause up to 3‰ enrichment in $\delta^{13}C_p$ (Madhavan et al., 1991). However, humidity effects are minimal in temperate deciduous plants (e.g. conifers; Franks and Farquhar, 1999), which likely formed a major portion of the diet in *Edmontosaurus* (Kräusel, 1922; Weishampel, 1984; Farlow, 1987; Norman and Weishampel, 1987; Chin and Gill, 1996). Without data on Late Cretaceous relative humidity levels for the bonebed site, it is difficult to assess the degree to which humidity might have affected $\delta^{13}C_e$ in *Edmontosaurus*.

In summary, enriched $\delta^{13}C_e$ values of *Edmontosaurus* can be explained by both environmental (i.e. high Late Cretaceous $\delta^{13}C_{atm}$ coupled with a diet of primarily gymnosperms and osmotically stressed plants) and physiological (i.e. a $\delta^{13}C_p$–$\delta^{13}C_{bioapatite}$ fractionation factor unique to dinosaurs) means, and are not therefore directly interpreted as diagenetic in nature. Based on the presence of an average C3 signal in $\delta^{13}C_{oc}$, we suggest that the most likely explanation is a combination of a diet of primarily gymnosperms and some osmotically stressed plants, and a unique dinosaurian $\delta^{13}C_p$–$\delta^{13}C_{bioapatite}$ biological fractionation factor. We are currently investigating the latter possibility. While preliminary and requiring further testing, these results suggest that vertebrate biogeochemists should take into account differing environmental and physiological variables that could affect "predicted" $\delta^{13}C$ values in any group of organisms lacking a close modern analog.

6. Conclusions

6.1. Diagenetic alteration in Edmontosaurus

Analyses of diagenesis in fossil dinosaur enamel, bone (cortical and cancellous), and dentine show a pattern of differential preservation in these tissues. Enamel is likely less altered than are bone and dentine based on (1) preservation of micro-scale crystalline structure in enamel, (2) heavier values in *Alligator* $\delta^{18}O_{ec}$ enamel versus *Edmontosaurus*, which is predicted if fossil enamel is unaltered, and (3) heavier $\delta^{18}O$ from bone and dentine than enamel, which is predicted if bone and dentine are more altered than enamel. The presence of $\delta^{18}O_{ec}$ variation in micro-sampled *Edmontosaurus* teeth is further evidence that original seasonal signals are preserved in enamel (i.e. that the *pattern* of seasonal variability is still apparent, even though *absolute* $\delta^{18}O_{ec}$ values may be altered).

Evidence for alteration of fossil bioapatite is shown from (1) greater variability in $\delta^{18}O_c$ than $\delta^{18}O_p$ (assuming $\delta^{18}O_p$ is unaltered), and (2) a non-linear correlation between $\delta^{18}O_p$ and $\delta^{18}O_c$ from co-existing replicates of enamel, dentine, and bone. However, the significance of this latter evidence is cast in doubt due to unanswered questions of dinosaurian biological fractionation patterns, the necessity of using a mammalian analog to determine the "expected" $\delta^{18}O_p$–$\delta^{18}O_c$ relationship, and the possibility that unaltered dinosaurian $\delta^{18}O_p$–$\delta^{18}O_c$ values have a different linear correlation than do mammals.

Based on the above evidence, we propose that the pattern of $\delta^{18}O_{ec}$ seasonal variability is preserved in *Edmontosaurus* enamel (although the absolute values are quite possibly less reliable) while dentine and bone are more heavily altered. Limited tests of diagenesis in $\delta^{13}C$ indicate that bone and dentine have undergone homogenization with marginal marine carbonates, while enamel has been affected to a lesser (albeit unquantified) degree.

6.2. Seasonal variation and tooth mineralization rates and times

Seasonal patterns of $\delta^{18}O_{ec}$ incorporation appear to be preserved in microsampled *Edmontosaurus* enamel. These signals indicate that teeth are mineralized year-round and not preferentially during a specific season. Based on the portion of a complete seasonal cycle preserved in microsampled enamel, all sampled teeth are interpreted as having been deposited in <0.65 year, with shorter mean mineralization times occurring in the juvenile and sub-adult specimens (with the exception of a single tooth in the juvenile). These estimates are broadly in agreement with, although slightly lower than, tooth formation times estimated by Erickson (1996b) using counts of growth lines in dentine. Discrepancies between estimates from the two methods are likely the result of differences in growth times of dentine and enamel, and/or preservational and sampling limitations in microsampled *Edmontosaurus* enamel.

Assessment of the length of enamel mineralized versus percent of the seasonal cycle represented by each tooth gives enamel mineralization rates of ~ 38 mm/year for *Edmontosaurus*, and 36 mm/year for modern *Alligator*. This is comparable to estimates of 40 mm/year in fossil bison and 21 mm/year in modern sheep (Fricke and O'Neil, 1996). Although *rates* of mineralization appear to be comparable, *timing* in archosaurs seems to be truncated because gross mineralization volume is greater in mammals than in *Edmontosaurus* and *Alligator* for a given period of time, as mammalian enamel is much thicker than is reptilian enamel.

It is unlikely that $\delta^{18}O_{ec}$ variability results from changes in ingested water $\delta^{18}O$ or from migratory effects, rather than localized seasonal variation. These behaviors would result in non-cyclical $\delta^{18}O$ patterns (in the case of source-water changes) and/or $\delta^{18}O$ homogenization (in the case of migration).

6.3. Paleodietary implications

Assuming a minimum of diagenetic alteration (see Section 5.1), more positive than predicted $\delta^{13}C_e$ values of *Edmontosaurus* specimens are interpreted as a combination of effects, including some or all of the following: (1) enrichment of dietary $\delta^{13}C_p$ due to higher overall $\delta^{13}C_{atm}$ in the Late Cretaceous, (2) more positive mean C3 $\delta^{13}C$ from ingested plants (interpreted as primarily gymnosperms) due to taxon-specific fractionation effects, (3) more positive than average $\delta^{13}C_p$ of ingested plants due to osmotic stress from proximity to brackish or saline water sources from the Western Cretaceous Interior Seaway; (4) taxon-specific fractionation factors for dinosaurs, who may not have possessed $\delta^{13}C_p - \delta^{13}C_{bioapatite}$ fractionation equivalent to that of mammals. While not discounting the possibility of diagenesis of $\delta^{13}C_e$, we consider dietary and taxon-specific fractionation factors to be the most likely explanation of enriched $\delta^{13}Ce$ values.

A lack of corroborating fossil evidence for the presence of C4 plants in the Late Cretaceous renders this explanation of enriched $\delta^{13}C_e$ values in *Edmontosaurus* unlikely. Similarly, explanations of heavy $\delta^{13}C_e$ values due to ingestion of CAM plants are unlikely, as pollen analysis of the *Edmontosaurus* bonebed shows no evidence of the presence of these plants.

6.4. General conclusions

Future studies will focus on analyzing isotope signatures in modern archosaur biominerals (i.e. birds and crocodilians) in an effort to further constrain ''expected'' physiological and ecological patterns found in dinosaur bioapatites. In order to evaluate the results of this analysis from an ecological perspective, isotopic comparisons of biominerals among multiple taxa from various sites on a coastal to upland transect will also be undertaken.

Diagenesis must be evaluated on a case-by-case basis, and such analysis is crucial to the defensible biological interpretations of stable isotope signals in fossil bioapatites. Preservation of original chemical and isotopic signatures in fossil bioapatite cannot be assumed.

This study provides a new perspective on hadrosaur physiology and ecology throughout ontogeny by analyzing microscale samples of the stable isotopes of tooth enamel. It suggests potentially important implications for future studies of growth rates in non-mammalian vertebrates, particularly other dinosaurs (e.g. ceratopsians and iguanodontids), and could serve as a model for these investigations.

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Appendix A

Data for all micro- and bulk-sampled enamel, dentine and bone from *Edmontosaurus*, *Alligator*, and ratites

Sample description	Bulk- or microsampled	$\delta^{18}O_p$ (VSMOW)	Intra $\delta^{18}O_p$ variability	Mean $\delta^{18}O_p$ per group	$\delta^{18}O_c$ (VSMOW)	Intra $\delta^{18}O_c$ variability	Mean $\delta^{18}O_c$ per group	$\delta^{13}C$ (VPDB)	Intra $\delta^{13}C$ variability	Mean $\delta^{13}C$ per group
Rhea Femur "A"	B	15.77			23.55			− 12.31		
Rhea Femur "B"	B	14.67			22.67			− 12.01		
Rhea Femur "C"	B	14.10			24.38			− 11.73		
Rhea Femur "D"	B	14.88	1.66	14.88	23.64	1.71	23.56	− 11.82	0.49	− 11.82
Ostrich Tibia "A"	B	14.08			22.61			− 8.92		
Ostrich Tibia "B"	B	13.79			23.02			− 8.40		
Ostrich Tibia "C"	B	13.46			22.05			− 10.22		
Ostrich Tibia "D"	B	13.58	0.62	14.67	22.05	0.97	22.43	− 8.31	1.91	− 10.88
Ostrich Femur "B"	B	13.61			23.03			− 9.94		
Ostrich Femur "C"	B	13.59			24.34			− 8.58		
Ostrich Femur "E"	B	13.89			23.06			− 8.46		
Ostrich Femur "F"	B	13.82	0.31	13.79	24.29	1.31	23.68	− 8.18	1.76	− 9.11
		Mean 14.10			Mean 23.22			Mean − 9.91		
		S.D. 0.68			S.D. 0.83			S.D. 1.65		
211-cortical dino bone	B	14.57			23.33			− 2.15		
211-cortical dino bone	B	14.03			22.54			− 1.94		
211-cancellous dino bone	B	14.15			22.72			− 2.74		
211-cancellous dino bone	B	14.55	0.54	14.38	23.13	0.79	22.93	− 0.82	1.92	− 1.64
2070-cortical dino bone	B	13.58			22.52			− 3.01		
2070-cortical dino bone	B	14.07			24.24			− 3.17		
2070-cortical dino bone	B	14.21			22.47			− 3.64		
2070-cancellous dino bone	B	14.61	1.03	14.09	22.84	1.77	23.02	− 1.57	2.07	− 2.58
207-cortical dino bone	B	14.65			23.51			− 2.21		
207-cortical dino bone	B	14.58			23.83			− 1.59		

Appendix A (*continued*)

Sample description	Bulk- or microsampled	$\delta^{18}O_p$ (VSMOW)	Intra $\delta^{18}O_p$ variability	Mean $\delta^{18}O_p$ per group	$\delta^{18}O_c$ (VSMOW)	Intra $\delta^{18}O_c$ variability	Mean $\delta^{18}O_c$ per group	$\delta^{13}C$ (VPDB)	Intra $\delta^{13}C$ variability	Mean $\delta^{13}C$ per group
207-cortical dino bone	B	14.37			24.04			− 2.52		
207-cancellous dino bone	B	14.56	0.28	14.59	23.28	0.76	23.66	− 1.30	1.22	− 1.70
1448-cancellous dino bone	B	14.39			23.62			− 1.16		
1448-cortical dino bone	B	14.50			20.44			− 3.27		
1448-cortical dino bone	B	14.34			23.60			− 2.39		
1448-cancellous dino bone	B	17.29	2.96	15.34	23.63	3.19	22.82	− 1.11	2.15	− 1.55
		Mean 14.53 S.D. 0.79			Mean 23.11 S.D. 0.90			Mean − 2.16 S.D. 0.86		
2070-tooth 1 dino dentine	B	13.22			24.97			0.66		
2070-tooth 2 dino dentine	B	13.36			22.37			0.15		
2070-tooth 3 dino dentine	B	14.01			23.59			0.75		
2070-tooth 4 dino dentine	B	13.16	0.85	14.00	23.10	2.60	23.64	1.26	1.11	− 1.47
207-tooth 1 dino dentine	B	13.75			22.82			1.04		
207-tooth 2 dino dentine	B	14.05			23.32			2.03		
207-tooth 3 dino dentine	B	13.64			23.25			0.19		
207-tooth 4 dino dentine	B	13.88	0.41	13.89	23.29	0.50	23.17	1.24	1.83	1.43
1448-tooth 0 dino dentine	B	13.55			22.17			1.57		
1448-tooth 0 dino dentine	B	13.82			24.13			1.02		
1448-tooth 1 dino dentine	B	13.27			20.18			2.25		
1448-tooth 2 dino dentine	B	13.75			22.04			3.22		
1448-tooth 3 dino dentine	B	13.78	0.55	13.73	23.02	3.95	22.31	2.28	2.20	1.68
		Mean 13.63 S.D. 0.30			Mean 22.94 S.D. 1.14			Mean 1.36 S.D. 0.89		
1448-0 dino enamel	B	12.27			19.78[a]					
1448-1 dino enamel	B	12.39			18.8[a]					
1448-2 dino enamel	B	12.35	0.12	12.33	19.59[a]	0.98	19.39			
2070-1 dino enamel	B	11.83			19.10[a]					

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Appendix A (*continued*)

Sample description	Bulk- or microsampled	$\delta^{18}O_p$ (VSMOW)	Intra $\delta^{18}O_p$ variability	Mean $\delta^{18}O_p$ per group	$\delta^{18}O_c$ (VSMOW)	Intra $\delta^{18}O_c$ variability	Mean $\delta^{18}O_c$ per group	$\delta^{13}C$ (VPDB)	Intra $\delta^{13}C$ variability	Mean $\delta^{13}C$ per group
2070-2 dino enamel	B	12.05	0.21	11.94	18.13[a]	0.96	18.62			
207-1 dino enamel	B	12.50			20.88[a]					
207-2 dino enamel	B	12.66	0.16	12.58	19.29[a]	1.59	20.09			
		Mean 12.29 S.D. 0.28			Mean 19.37 S.D. 0.86					
Gator enamel, tooth 7A, Position 1	M	n/a			25.15			− 14.51		
Gator enamel, tooth 7A, Position 2	M	n/a			24.50			− 14.41		
Gator enamel, tooth 7A, Position 3	M	n/a			24.49			− 13.95		
Gator enamel, tooth 7A, Position 4	M	n/a			24.39			− 13.87		
Gator enamel, tooth 7A, Position 5	M	n/a			24.81			− 14.11		
Gator enamel, tooth 7A, Position 7	M	n/a			24.62	0.76	24.66	− 13.20	1.31	− 14.01
					Mean 24.66 S.D. 0.28			Mean − 14.01 S.D. 0.47		
Gator enamel, tooth 7B, Position 1	M	n/a			25.25			− 12.12		
Gator enamel, tooth 7B, Position 2	M	n/a			23.91			− 12.03		
Gator enamel, tooth 7B, Position 3	M	n/a			23.32	1.93	24.16	− 12.49	0.46	− 12.21
					Mean 24.16 S.D. 0.99			Mean − 12.21 S.D. 0.24		
Gator enamel, tooth 8A, Position 1	M	n/a			24.45			− 15.14		
Gator enamel, tooth 8A, Position 2	M	n/a			24.50			− 14.67		
Gator enamel, tooth 8A, Position 3	M	n/a			24.35			− 14.48		

Appendix A (*continued*)

Sample description	Bulk- or microsampled	$\delta^{18}O_p$ (VSMOW)	Intra $\delta^{18}O_p$ variability	Mean $\delta^{18}O_p$ per group	$\delta^{18}O_c$ (VSMOW)	Intra $\delta^{18}O_c$ variability	Mean $\delta^{18}O_c$ per group	$\delta^{13}C$ (VPDB)	Intra $\delta^{13}C$ variability	Mean $\delta^{13}C$ per group
Gator enamel, tooth 8A, Position 4	M	n/a			24.53			− 14.70		
Gator enamel, tooth 8A, Position 5	M	n/a			25.32			− 13.74		
Gator enamel, tooth 8A, Position 6	M	n/a			24.79	0.97	24.66	− 13.22	1.92	− 14.33
					Mean 24.66 S.D. 0.36			Mean − 14.33 S.D. 0.71		
Gator enamel, tooth 8B, Position 1	M	n/a			25.65			− 11.87		
Gator enamel, tooth 8B, Position 2	M	n/a			24.57			− 12.30		
Gator enamel, tooth 8B, Position 3	M	n/a			25.12			− 12.09		
Gator enamel, tooth 8B, Position 4	M	n/a			24.13			− 12.12		
Gator enamel, tooth 8B, Position 5	M	n/a			23.34	2.31	24.56	− 12.27	0.43	− 12.13
					Mean 24.56 S.D. 0.89			Mean − 12.13 S.D. 0.17		
1448-tooth 0 dino enamel	M/B				18.88			− 3.54		
1448-tooth 0 dino enamel	M/B	12.27			20.67	1.79	19.78	− 2.35	1.19	− 2.95
					Mean 19.775 S.D. 1.27			Mean − 2.945 S.D. 0.84		
1448-tooth 1 dino enamel	M/B				18.08			− 3.34		
1448-tooth 1 dino enamel	M/B				18.6			− 3.3		
1448-tooth 1 dino enamel	M/B	12.39			19.73	1.65	18.80	− 3.22	0.12	− 3.29
					Mean 18.80 S.D. 0.84			Mean − 3.29 S.D. 0.06		
1448-tooth 2 dino enamel	M/B				17.68			− 3.3		
1448-tooth 2 dino enamel	M/B				19.75			− 0.55		
1448-tooth 2 dino enamel	M/B				19.84			− 1.06		

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Appendix A (*continued*)

Sample description	Bulk- or microsampled	$\delta^{18}O_p$ (VSMOW)	Intra $\delta^{18}O_p$ variability	Mean $\delta^{18}O_p$ per group	$\delta^{18}O_c$ (VSMOW)	Intra $\delta^{18}O_c$ variability	Mean $\delta^{18}O_c$ per group	$\delta^{13}C$ (VPDB)	Intra $\delta^{13}C$ variability	Mean $\delta^{13}C$ per group
1448-tooth 2 dino enamel	M/B	12.35			19.49	2.16	19.19	− 1.68	2.75	− 1.6
					Mean 19.19 S.D. 1.02			Mean − 1.65 S.D. 1.19		
1448-tooth 3 dino enamel	M				20.52			− 0.1		
1448-tooth 3 dino enamel	M				18.27			− 2.75		
1448-tooth 3 dino enamel	M				18.00	2.52	18.93	− 3.28	3.18	− 2.04
					Mean 18.93 S.D. 1.38			Mean − 2.04 S.D. 1.70		
207-tooth 1 dino enamel	M/B				23.18			− 1.46		
207-tooth 1 dino enamel	M/B				23.61			− 1.48		
207-tooth 1 dino enamel	M/B				20.66			− 2.42		
207-tooth 1 dino enamel	M/B				19.87			− 3.03		
207-tooth 1 dino enamel	M/B				18.76			− 3.88		
207-tooth 1 dino enamel	M/B	12.50			19.22	4.85	20.88	− 3.76	2.42	− 2.67
					Mean 20.88 S.D. 2.05			Mean − 2.67 S.D. 1.07		
207-tooth 2 dino enamel	M/B				20.23			− 3.12		
207-tooth 2 dino enamel	M/B				19.38			− 3.81		
207-tooth 2 dino enamel	M/B				18.78			− 4.29		
207-tooth 2 dino enamel	M/B	12.66			18.77	1.47	19.29	− 4.02	1.18	− 3.81
					Mean 19.29 S.D. 0.69			Mean − 3.81 S.D. 0.50		
207-tooth 3 dino enamel	M				19.58			− 3.93		
207-tooth 3 dino enamel	M				19.08	0.51	19.33	− 4.85	0.92	− 4.39
					Mean 19.33 S.D. 0.36			Mean − 4.39 S.D. 0.65		
207-tooth 4 dino enamel	M				19.18	n/a	n/a	− 4.16	n/a	− 4.16
2070-tooth 1 dino enamel	M/B				18.91			− 4.66		
2070-tooth 1 dino enamel	M/B				18.78			− 4.38		
2070-tooth 1 dino enamel	M/B				20.04			− 3.88		

Appendix A (*continued*)

Sample description	Bulk- or microsampled	$\delta^{18}O_p$ (VSMOW)	Intra $\delta^{18}O_p$ variability	Mean $\delta^{18}O_p$ per group	$\delta^{18}O_c$ (VSMOW)	Intra $\delta^{18}O_c$ variability	Mean $\delta^{18}O_c$ per group	$\delta^{13}C$ (VPDB)	Intra $\delta^{13}C$ variability	Mean $\delta^{13}C$ per group
2070-tooth 1 dino enamel	M/B				18.75			−4.91		
2070-tooth 1 dino enamel	M/B	11.83			19.00	1.29	19.10	−4.46	1.04	−4.46
					Mean 19.10 S.D. 0.54			Mean −4.46 S.D. 0.38		
2070-tooth 2 dino enamel	M/B				17.56			−6.69		
2070-tooth 2 dino enamel	M/B				18.28			−6.10		
2070-tooth 2 dino enamel	M/B				17.92			−6.24		
2070-tooth 2 dino enamel	M/B				19.34			−5.20		
2070-tooth 2 dino enamel	M/B	12.05			17.57	1.78	17.57	−6.69	1.49	−6.18
					Mean 18.13 S.D. 0.74			Mean −6.18 S.D. 0.61		
2070-tooth 3 dino enamel	M				18.09			−6.06		
2070-tooth 3 dino enamel	M				18.02			−6.51		
2070-tooth 3 dino enamel	M				17.83			−6.92		
2070-tooth 3 dino enamel	M				17.47	0.61	17.85	−7.10	1.03	−6.65
					Mean 17.85 S.D. 0.28			Mean −6.65 S.D. 0.46		
2070-tooth 4 dino enamel	M				20.87			−3.62		
2070-tooth 4 dino enamel	M				19.25			−5.28		
2070-tooth 4 dino enamel	M				19.96	1.62	20.03	−4.35	1.66	−4.42
					Mean 20.03 S.D. 0.812			Mean −4.42 S.D. 0.83		

[a] Calculated as mean values from microsampled specimens.

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