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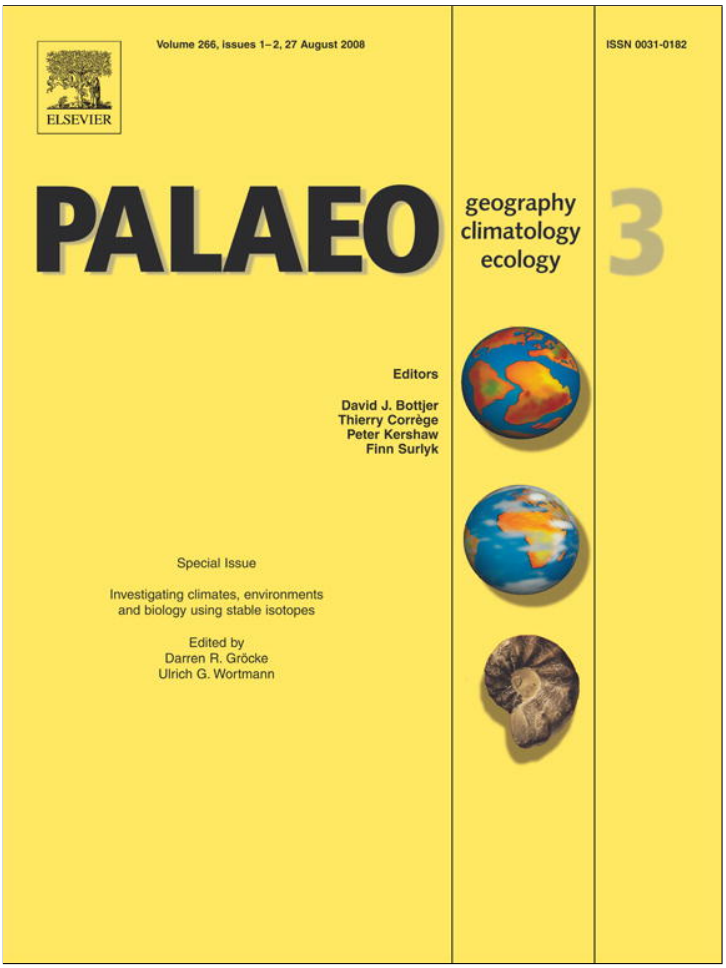

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Preservation of primary stable isotope signals in dinosaur remains, and environmental gradients of the Late Cretaceous of Montana and Alberta

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ABSTRACT

Although the use of stable isotope data from vertebrate remains is becoming common for the Cenozoic, their application to Mesozoic environments has been rare, in part due to the perception that diagenesis has obfuscated all potential primary signal. In this paper, we illustrate how stable isotope data collected from dinosaur and other vertebrate remains can in fact be used to reconstruct paleoenvironmental conditions during the Mesozoic.

Carbon and oxygen isotope ratios were measured from tooth enamel of hadrosaur dinosaurs and from scales of freshwater fish that were collected from sites in the Two Medicine, Judith River, and Dinosaur Park Formations of Montana and Alberta. These formations represent a coastal to upland gradient along the western margin of the Late Cretaceous inland seaway. Isotopic comparisons among skeletal components and among taxa are used as evidence that primary paleoenvironmental information, as recorded by isotope data, is preserved in tooth enamel and freshwater fish scales. A comparison of carbon isotope ratios between hadrosaur tooth enamel and sedimentary organic matter indicates that these animals had a larger isotopic offset compared to bulk diet than modern mammals, and that all hadrosaurian isotope data are consistent with the existence of C_3-only ecosystems.

Higher and more variable carbon and oxygen isotope ratios from animals occupying the coastal Judith River region are interpreted to reflect a range of freshwater to brackish water conditions and plants that were undergoing water stress. Lower and less variable carbon and oxygen isotope ratios from the upland Two Medicine and intermediate Dinosaur Park areas are interpreted to reflect a gradual rainout of moisture from air masses moving inland and more uniform environmental conditions. Overall, these results indicate that stable isotopes from dinosaur and other vertebrate remains have the potential to expand our understanding of terrestrial environments and ecosystems during the Mesozoic.

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1. Introduction

Dinosaurs have been the focus of intense scientific interest for well over 150 years, yet many aspects of their ecology and behavior remain enigmatic. For example, the dietary preferences of most dinosaurs remain unknown, as do their interactions with other vertebrates and plants. To address these kinds of questions, paleontologists have traditionally relied on studies of skeletal morphology and biogeography, along with rare insights from coprolites, tooth marks, and preserved gut contents (e.g. Chin et al., 1998; Varricchio, 2001; Rogers et al., 2003a,b). For example, teeth can provide valuable information on gross type of dietary behavior, such as carnivory or herbivory. Similarly, overall body size can allow inferences to be made regarding type of plants preferred by herbivorous taxa, with tall or long-necked taxa potentially eating plants of the forest canopy, and smaller animals relying on understory vegetation. The paleogeographic distribution of dinosaur fossils in relation to depositional environments can also provide general information about preferred habitats (e.g. Lehman, 1987). These types of studies, however, are indirect, in that they are based on modern morphological analogs and the stratigraphic and geographic distributions of fossils, which are to some extent moderated by taphonomic processes.

As a complement to these traditional studies, geochemical investigations of fossil remains and associated authigenic minerals have the potential to provide both direct and indirect information regarding preferred habitats and general environmental conditions of the past (see reviews of Koch, 1998; Kohn and Cerling, 2002; Lee-Thorp and Sponheimer, 2005; Fricke, 2007). To date, such analysis has focused almost exclusively on mammals living during the Cenozoic. Data have been used to study climatic conditions vegetation structure, ecological relations and niche partitioning, and rates of dental development (Koch, 1998; Kohn and Cerling, 2002; Lee-Thorp and Sponheimer, 2005; Fricke, 2007). The main goal of this paper is to demonstrate that similar kinds of paleoenvironmental investigations can be undertaken for Mesozoic time periods using stable isotope data from carbonate in dinosaur tooth

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enamel. In particular, we undertake several different kinds of isotopic comparisons to provide evidence that, even if affected by diagenetic processes to some extent, primary and interpretable isotopic information is preserved in vertebrate remains (hadrosaur and fish) from the Late Cretaceous.

With indication that primary isotopic information is preserved, carbon and oxygen isotope data from hadrosaurs are then considered in the context of an existing paleoenvironmental framework that is based on independent sedimentological data. The result indicates that differences in stable isotope ratios do track shifts in depositional environments and their position relative to the coast of the inland seaway.

2. Background — carbon, oxygen, tooth enamel and dinosaurs

One primary reason that stable isotope ratios can be used for studying environments of the past is that carbon isotope ratios of plants change in response to the type of photosynthetic pathways utilized by the plant and to environmental conditions (O'Leary, 1988; Farquhar et al., 1989; O'Leary et al., 1992). Plants using the C_3 (Calvin) pathway presumably dominated Mesozoic ecosystems (Cerling, 1999), and are characterized by a large isotopic discrimination between organic material and CO_2 in the atmosphere. The result is that carbon isotope ratios of C_3 plants range from ~−32 to −21‰ with an average of ~−26‰ compared to ~−8‰ for modern atmospheric CO_2. Some of this isotopic variability in C_3 plants reflects differing isotopic discrimination for different taxa, with plants such as gymnosperms typically having higher $\delta^{13}C$ values than others (Tieszen, 1991; Heaton, 1999). Environmental conditions can also cause carbon isotope ratios of specific C_3 plants to vary because they are very sensitive to the amount of CO_2 in a leaf cell. In turn, concentrations of CO_2 in a leaf cell are influenced a great deal by the opening and closing of leaf stomata, which controls the flux of CO_2 into the plant. Stomata are more likely to remain closed when environmental factors such as temperature, water availability, salinity, nutrient availability and light intensity are such that water needs to be conserved (O'Leary, 1988; Farquhar et al., 1989; Tieszen, 1991; O'Leary et al., 1992). A summary of environmental effects is provided by Heaton (1999). The location of a plant under a closed forest canopy can also affect carbon isotope ratios of plant material as CO_2 in these setting exhibits lower carbon isotope ratios than the open atmosphere due to plant respiration and decomposition on or near the forest floor. When incorporated into understory plants during photosynthesis, the lower carbon isotope ratios stand out in comparison to the same plants living in open canopy settings (e.g. van der Merwe and Medina, 1991; Cerling et al., 2004). Lastly, if the carbon isotope ratio of atmospheric CO_2 changes over time, that of plant material forming from it will also change.

Oxygen isotope ratios of waters in streams, lakes, and leaves also vary significantly in response to environmental factors such as temperature and aridity, and to the hydrological 'history' of air masses that are supplying precipitation to these surface water reservoirs (Epstein and Mayeda, 1953; Dansgaard, 1964; Rozanski et al., 1993; Gat, 1996). At present, oxygen isotope ratios of global precipitation ranges from ~0 to −30‰ (Dansgaard, 1964; Rozanski et al., 1993). The primary cause of isotopic variability in precipitation is the preferential incorporation of ^{18}O into condensate as water is precipitated and removed from cooling air masses. The resulting patterns in oxygen isotope ratios of precipitation include a regular decrease as air masses cool while rising over mountains, moving away from coastal areas, or moving from tropical source areas to polar sinks (Epstein and Mayeda, 1953; Dansgaard, 1964; Rozanski et al., 1993; Gat, 1996). In tropical regions, where vertical convection results in cooling, a correlation also occurs between the amount of precipitation and oxygen isotope ratios of precipitation (Dansgaard, 1964; Araguas-Araguas et al., 1998).

Although regional temperatures and rainout patterns play a major role in determining the oxygen isotope ratio of precipitation at any given locality, terrestrial vertebrates generally do not ingest precipitation directly. Instead, they ingest water from surface water reservoirs such as streams, lakes, and leaves. In turn, these reservoirs may have oxygen isotope ratios that differ significantly from those of local precipitation due to a variety of local hydrological processes. For example, ponds and streams in humid areas may hold local precipitation with little isotopic modification, but larger lakes and soil waters, especially in arid regions, may undergo evaporation that modifies their oxygen isotope ratio via the preferential incorporation of ^{16}O into the vapor phase. Similarly, oxygen isotope ratios of leaf water ingested by herbivorous animals can be shifted to higher values relative to precipitation as a result of evaporation at the surface of a leaf, particularly in less-humid environments (Sternberg, 1989). Lastly, precipitation from large areas and over long periods of time can be mixed together during the formation of lakes, soil and ground waters, and larger rivers.

Animals record the isotopic characteristics of ancient landscapes when they ingest organic material and drink from surface water reservoirs and then form bioapatite [$Ca_5(PO_4, CO_3)_3(OH, CO_3)$], which is a major component of tooth enamel, tooth dentine, bone, and body scales of some fish and reptiles. Carbon found in the carbonate phase of bioapatite is related to ingested organic material, such as plants in the case of herbivores and flesh in the case of carnivores. After being eaten by an herbivore, organic compounds in plants are metabolized and carbon is incorporated into a number of different phases, including dissolved CO_2 and HCO_{3-}, which ultimately come to reside in the herbivore's bioapatite (see Koch et al., 1994; Koch, 1998; Cerling and Harris, 1999; Passey et al., 2005). Carbon isotope fractionations associated with these processes result in carbon isotope ratios of bioapatite carbonate higher than those of ingested plant matter.

Oxygen in vertebrate bioapatite has sources primarily in ingested water and atmospheric oxygen that contribute to blood/metabolic water (Longinelli 1984; Luz and Kolodny, 1985; Bryant and Froelich, 1995; Kohn, 1996; Kohn and Cerling, 2002). The oxygen isotope ratio of atmospheric oxygen has remained relatively constant over time and space with a value of ~23‰ (Kohn, 1996). Thus it probably does not influence oxygen isotope *variations* in bioapatite of vertebrates living in different places or drinking different waters. The isotopic offset between ingested surface water and both phosphate and carbonate phases that are present in biogenic apatite is controlled by (1) body temperature, which determines the isotopic fractionation between apatite and body water, and (2) fractionations that occur during the formation of body water from ingested water. Where body temperatures are known and constant (i.e. homeothermic mammals and birds), both of these factors can be considered together using physiological models that account for the fluxes of oxygen into and out of the body of an animal, and the oxygen isotope fractionations associated with each metabolic process (Bryant and Froelich, 1995; Kohn, 1996). Alternatively, direct empirical relations between oxygen isotope ratios of bioapatite and those of meteoric water may be used for different kinds of animals (e.g. Koch, 1998; Iacumin and Longinelli, 2002; Kohn and Cerling, 2002; Hoppe et al., 2004; Hoppe, 2006).

To date, stable isotope ratios of dinosaur remains have not been used extensively to study environmental conditions of the Mesozoic. Part of the reason is that such studies are complicated by the fact that isotopic relations between ingested carbon and oxygen and tooth enamel carbon and oxygen have not been determined precisely for Mesozoic animals. For example, in one of the most thorough studies of Late Cretaceous dinosaurs living in one place, Stanton-Thomas and Carlson (2003) were not able to make definitive interpretations of their carbon isotope data from hadrosaurs because they did not know the carbon isotope offset between tooth enamel carbonate and diet. As a result, these authors could not discount diagenetic alteration of isotope ratios, or the possible existence of plants with non-C_3 photosynthetic pathways (i.e. those with C_4 and CAM pathways) when evaluating their data. In the case of oxygen, both exact body

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temperatures and metabolic fractionations are unknown, and interpreting oxygen isotope data obtained from dinosaurs is difficult.

Despite these difficulties in interpreting stable isotope data from a single dinosaur taxon living in one place, a few basic assumptions can be made that open up a number of different research opportunities. One assumption is that all dinosaurs utilized carbon in the same basic way as extant vertebrates such as birds, reptiles, and mammals, in particular that carbon found in bioapatite has a source in ingested organic material. It is also reasonable to assume that all dinosaurs utilized oxygen in the same basic way as extant vertebrates, and therefore that oxygen in their bioapatite had sources primarily in ingested water and atmospheric oxygen. Furthermore, several isotopic studies of dinosaur and coexisting reptile remains indicate that they were able to maintain relatively constant body temperatures (Barrick and Showers, 1994, 1995; Barrick et al., 1996; Fricke and Rogers, 2000), even if these temperatures could not be determined exactly. Lastly, for any given dinosaur taxon it is reasonable to assume that the basic physiological controls on the utilization of carbon and oxygen did not vary significantly over time or space.

Using these assumptions, it is possible to interpret *relative differences* in isotope ratios among Mesozoic data sets, in particular isotopic differences *among taxa* from the same locality and isotopic differences for the same taxon *recovered from different localities*, as reflecting primary (ancient) isotopic differences in ingested food and water. In the case of carbon, any difference among remains of the same taxon found in different places will reflect differences in plant type eaten or in micro-environment occupied by the animal, while carbon isotope differences among taxa living in one place (sampled from one localized facies) should reflect different physiologies, diets, or other behaviors (e.g. Botha et al., 2005). Similarly, for oxygen, isotopic differences among taxa, or among the same taxon living in different places or times should reflect differences in oxygen isotope ratios of ingested water only, and can be used to study animal behaviors or environments of the past. For example, oxygen isotope data derived from theropod remains over a broad latitudinal transect indicate that temperature gradients for the Late Cretaceous were shallower than at present (Amiot et al., 2004). Along these same lines, Straight et al. (2004) used oxygen isotope data derived from theropod tooth enamel to reveal seasonal patterns in rainfall and humidity in Alberta during the Late Cretaceous.

3. Diagenesis

Diagenesis, or the chemical alteration of bioapatite after the death of an animal, is something that has likely affected all fossilized material. Because several studies have indicted that such alteration can occur relatively soon after burial (e.g. Trueman and Tuross, 2002), it is critical to evaluate the impact of diagenetic processes on stable isotope ratios of all fossil bioapatite, including that of both Cenozoic and Mesozoic ages. Unfortunately, no method described to date can provide unambiguous evidence whether isotopic alteration has or has not occurred in fossil bioapatite (e.g. Kohn and Cerling, 2002). As a result, our goal here is *not* to demonstrate that isotopic alteration is absent. Rather, our goal is to demonstrate that diagenesis has not entirely obscured original paleoenvironmental, paleoecological and/or paleobiological information that is reflected in stable isotope ratios of biogenic apatite. In this case, we feel that by comparing related isotopic data (1) between enamel and authigenic carbonate, (2) between enamel and dentine from the same fossil element, and (3) between vertebrate taxa, it is possible to make a strong case that original isotopic information is still preserved to some degree in enamel carbonate.

To understand the rationale for comparing different isotopic data sets, a basic knowledge of diagenetic processes, and how these relate to physical and chemical variations within bioapatite, is necessary. In this paper, our focus is on carbon and oxygen isotope data that can be obtained from the carbonate component of bioapatite. Many of the basic concepts, however, can be applied to oxygen isotope data from the phosphate component as well. In general, diagenetic alteration of bioapatite occur by two end-member processes: (1) isotopic exchange between biogenic apatite and surrounding fluids containing H_2O, HCO_3–, CO_2, CH_4, and (2) dissolution and/or addition of secondary apatite and carbonate (e.g. Zazzo et al., 2004). The former requires that C–O bonds of anionic complexes within apatite be broken and then reformed so that isotope exchange may occur. In addition, for the isotope ratio of carbonate in recrystallized apatite to differ significantly from initial ratios, the temperature of this process must be significantly different than that of formation, or isotopic exchange must occur in the presence of C and O from an external source that has an isotope ratio much different than that found in the primary carbonate complex.

In the case of secondary mineral precipitation, biogenic apatite may retain its original isotope ratios, but this primary signal can be overwhelmed. Secondary carbonate minerals may precipitate from ground waters that are isotopically much different than body water, and at temperatures that are much different than those in the body of an animal. As a result, isotope ratios of secondary minerals may not be the same as those of unaltered biogenic apatite, and the degree of isotopic alteration observed will depend on the percentage of secondary mineral present.

What follows from this overview is that skeletal remains with high porosities may be subjected to greater fluxes of exogenous fluids, while those with smaller apatite crystals have much more surface area available to undergo isotopic exchange and more volume available for precipitation of secondary phosphates and carbonates. Of the common skeletal materials, bone has very small apatite crystals tens of nanometers in length, and a framework of organic collagen that makes up ~30% of unaltered bone (Hillson, 1986). Tooth dentine and the dentine-like material underlying garfish scales is characterized by similar crystal sizes, but less collagen. In contrast, enamel and the homologous ganoine of some fish scales are made up of larger apatite crystals hundreds of nanometers in length, and only contains <3% original organic material (Hillson, 1986; Zylberberg et al., 1997). Organic collagen is likely to be altered or removed early after burial thus providing a pathway for fluids. As a result bone is most likely to be susceptible to diagenetic processes (Nelson et al., 1986; Kolodny et al., 1996; Kohn and Cerling 2002; Trueman et al., 2003), tooth dentine is less so, and tooth enamel and scale ganoine are least likely to be affected.

In addition to biogenic apatite, it is also possible that sedimentary organic matter may be altered isotopically so that carbon isotope ratios of this material no longer reflect that of original plant material. In particular, it has been observed that ^{12}C is often preferred by microbial organisms living in modern soils and peatland sediments similar to those inferred for the Late Cretaceous, and this ^{12}C can be exported from the system via organic decomposition and methane production (e.g. Herczeg, 1988; Hornibrook et al., 2000). As a result, remaining carbon in sedimentary organic matter can have higher $\delta^{13}C$ (e.g. Krull and Skjemstad, 2003; Wynn et al., 2005).

4. Geologic setting and materials

One way to test whether stable isotope ratios from vertebrate remains preserve primary information is to analyze samples from multiple well-constrained fossil localities where significant differences in environmental conditions are already documented. In this regard, the Upper Cretaceous Two Medicine and Judith River formations of Montana (TMF and JRF) and the Dinosaur Park Formation (DPF) of Alberta provide an ideal setting. For all three formations collection and analysis of fossil material can be conducted in a preexisting stratigraphic framework (Eberth and Hamblin, 1993; Rogers, 1994, 1995; 1998; Eberth, 2005), and teeth and scales from a wide array of vertebrates can be obtained from a suite of known

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localities that represent both semi-arid upland settings and more humid coastal plain paleoenvironments (Brinkman, 1990; Eberth, 1990; Rogers, 1990, 1993; Rogers and Kidwell, 2000). The key point is that deposits of the alluvial uplands (TMF) can be correlated and compared with comparably aged facies of the coastal plain lowlands (JRF and DPF) (see Fig. 1).

The TMF, JRF, and DPF are richly fossiliferous, and each formation preserves a variety of skeletal concentrations (macrofossil and microfossil bonebeds) set in a background of dispersed skeletal material (Brinkman, 1990; Eberth, 1990; Rogers, 1993, 1995; Rogers and Kidwell, 2000; Eberth, 2005). These concentrations include dinosaur nests and nesting horizons, dinosaur bonebeds dominated by large elements (Rogers, 1990, 1995; Varricchio, 1995; Ryan et al., 2001), and diverse microfossil bonebeds (microsites) of both terrestrial and marine origin (e.g. Eberth, 1990; Brinkman, 1990; Rogers, 1995; Rogers and Kidwell, 2000). Microfossil bonebeds, which typically consist of small physicochemically resistant elements such as teeth, scales, scutes, and compact bones (phalanges, vertebrae), are particularly abundant within the study interval, and accordingly this category of bonebed provided the fossil material for our isotopic analyses (see below). These types of sites, with their great

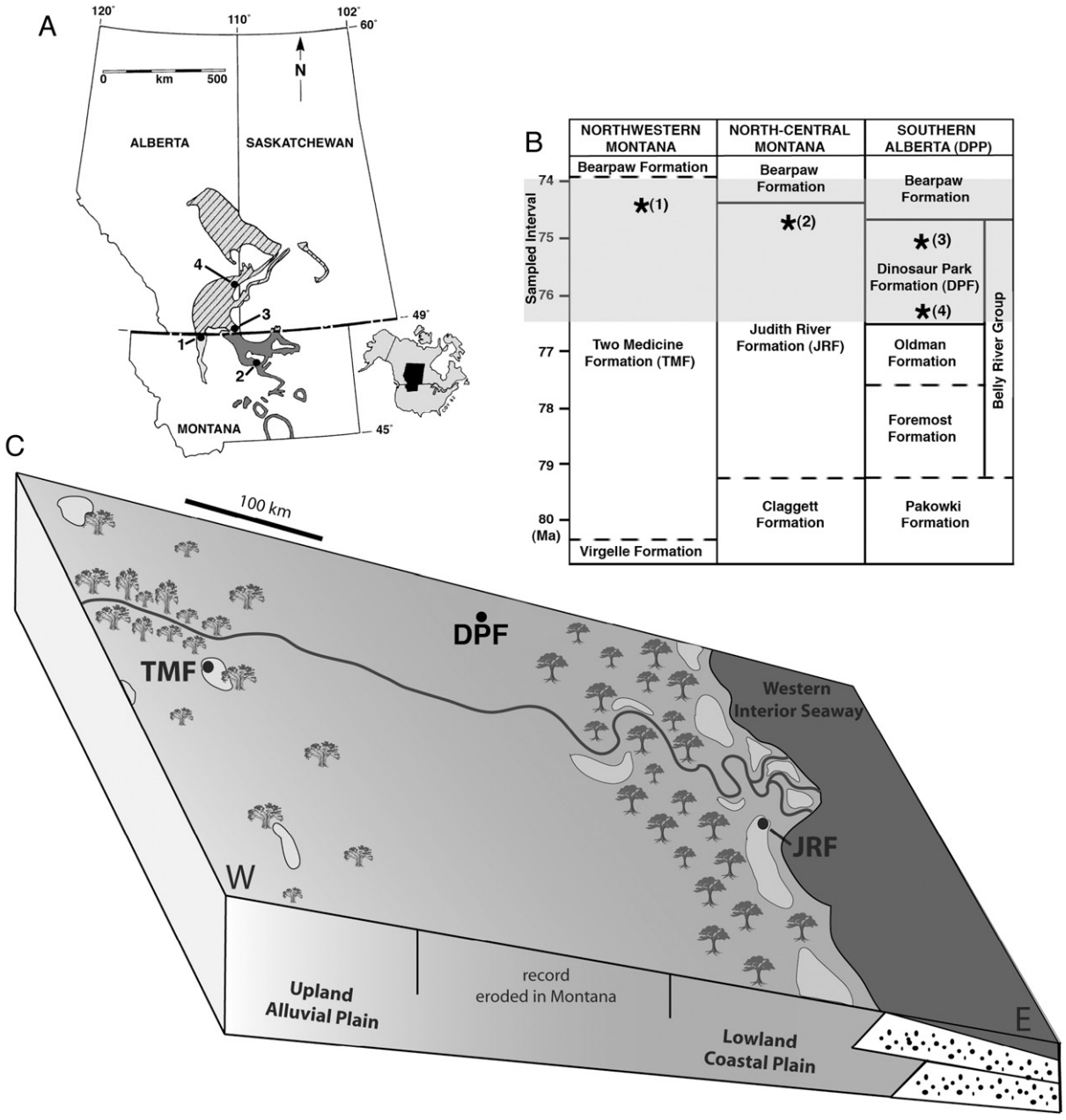

Fig. 1. (A) Location map of localities sampled in this study (modified from Eberth and Hamblin, 1993). Locality 1 is the Landslide Butte field area (Rogers, 1990) in the upper portion of the Two Medicine Formation (TMF, light gray) in northwestern Montana. Localities sampled in this field area include TM-020, TM-053, TM2, and TM4. Locality 2 (UC-8303: Rogers, 1995) is situated in the upper Judith River Formation (JRF, dark gray) in its type area along the Missouri River in north-central Montana. Localities 3 (Millar Bonebed) and 4 (Matt's Site) occur in the Dinosaur Park Formation (DPF) in southern Alberta (hachured pattern in Alberta and Saskatchewan delimits outcrop belt of Judith River Group). (B) Correlation chart of formations and localities sampled in this study (based on Rogers et al., 2003a,b; Eberth, 2005). Localities range in age from 74 to 76.5 Ma. (C) Schematic diagram illustrating paleogeographic positions of localities in the TMF (alluvial "uplands"), JRF (shoreline proximal coastal plain lowlands, stipple pattern indicates shoreface), and DPF (intermediate "upper coastal plain"). Hadrosaur taxa documented in the study interval (Weishampel et al., 2004) include: TMF (*Maiasaura peeblesorum*, *Prosaurolophus blackfeetensis*, *Hypacrosaurus stebingeri*, *Gryposaurus* sp., and indeterminate forms), JRF (*Brachylophosaurus canadensis*, *Brachylophosaurus* sp., and several indeterminate forms), DPF (*Brachylophosaurus canadensis*, *Gryposaurus notablis*, *Gryposurus incurvimanus*, *Prosaurolophus maximus*, *Corythosaurus casuarius*, *Lambeosaurus lambei*, *Lambeosaurus magnicristatus*, *Parasaurolophus walkeri*, *Maisaura* sp.?, and several indeterminate forms).

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abundance of dissociated skeletal material, are ideal for the comparative approach we followed, because from a taphonomic perspective (see Badgley, 1986) each specimen analyzed can be assumed to represent a distinct individual unless association among elements can be demonstrated (e.g. matching breaks on two separate specimens). Moreover, the sheer abundance of fossil material, coupled with the fact that fossils tend to occur in a dissociated state, renders it more likely that fossils from microfossil bonebeds will be made available for destructive analysis.

From a paleoenvironmental perspective, the portion of the TMF targeted in this study (Fig. 1) represents fluvial and floodplain deposits of the alluvial "uplands" (upland is used herein as indicative of being 100's km distant from the coeval shoreline of the Cretaceous Interior Seaway). Sedimentological features, including oxidized paleosols that yield pedogenic carbonate nodules, indicate that the TMF generally represents a more arid depositional setting (Rogers, 1998). Taphonomic studies are consistent with this interpretation (Rogers, 1990; Varricchio, 1995), and indicate that the TMF ecosystem was likely susceptible to occasional droughts (also see Falcon-Lang, 2003). The four sites from the TMF analyzed in this study (TM-020, TM-053, TM2, TM4) are all located in the Landslide Butte field area (Rogers, 1990), and all are positioned within the upper 90 m of the formation. Their proximity to the overlying biostratigraphically zoned marine shales of the Bearpaw Formation (Gill and Cobban, 1973), coupled with radioisotopic data derived from stratigraphically equivalent beds in the Two Medicine Formation type area (Rogers et al., 2003a,b), indicate that these sites are late Campanian in age.

In contrast to the upland derivation of the Two Medicine fossils, vertebrate skeletal debris from the JRF analyzed in this study accumulated in the coastal plain lowlands amidst tidally influenced fluvial channels, swampy fluvial backwaters, shallow floodbasin ponds and lakes, and hydromorphic soils (Fig. 1). Stratigraphic data indicate that the locality sampled (UC-8303) was positioned within 10 km of contemporaneous shoreface deposits, and thus presumably rested in close proximity to the paleoshoreline (Rogers, 1998). Sedimentological features and fossils, including small freshwater bivalves and gastropods, indicate that the UC-8303 fossil assemblage accumulated in a shallow subaqueous setting. The abundance of flatly laminated carbonaceous debris indicates that the low-energy burial environment was reducing. Recent radioisotopic analyses in the Judith River Formation type area definitively place the UC-8303 locality in the late Campanian (Rogers, 1998).

Finally, from a paleogeographic perspective, the two sites sampled from the DPF in southern Alberta (Matt's Site, Millar Bonebed) can be considered intermediate in location relative to the TMF and JRF localities (Fig. 1C). Both DPF localities definitely accumulated in coastal plain facies downdip from the more arid alluvial "uplands" of the TMF. Moreover, both sites accumulated inland from the coastal setting of UC-8303 in the JRF, with current estimates placing Matt's Site ~150 km updip from the paleoshoreline (D. Eberth, pers. comm., 2007). The age of the DPF localities ranges from ~76.5 Ma (Matt's Site) to ~75 Ma (Millar's Bonebed) (D. Eberth, pers. comm., 2007).

5. Methods and results

Hadrosaur teeth (both intact shed specimens and fragments), ganoid gar scales, and invertebrate shell fragments were recovered from microfossil bonebeds via both surface collection and screening. Teeth were not identified beyond the family level (Hadrosauridae), and therefore it is possible that teeth from multiple species within this major group were analyzed together. It is also important to note, however, that there is relatively little overlap of hadrosaur taxa among the formations under study (Weishampel et al., 2004). For example, none of the presently known hadrosaur species from the TMF are known to occur in the correlative facies of the JRF (Weishampel et al., 2004). There was no attempt to identify ganoid fish scales beyond Lepisosteidae (referred to as "gar" in this paper) or invertebrate shell material beyond Mollusca. Mineralogical analysis of invertebrate shell material was conducting using a Phillips 1710 X-ray diffractometer at Colorado College.

In addition to fossils, bulk sediment was collected from each microfossil bonebed, as well as from multiple horizons stratigraphically above and below each bonebed. Paleosol carbonates were also collected from the Two Medicine Formation. No other authigenic carbonates (e.g. spar, micrite, etc.) were found in any of the other sediments or fossils studied.

Samples were taken for analysis from paleosol carbonates and from different skeletal components using a Dremel drill with diamond-tipped bits. These skeletal components include dentine and enamel from dinosaur teeth, dentine and ganoine from gar scales, and invertebrate shells. Enamel and ganoine thickness varied from element to element, but both generally range from 0.5 to 1.5 mm. Carbon and oxygen isotope ratios of ingested plant matter and water likely varied seasonally by a few per mil (Fricke and O'Neil, 1996; Sharp and Cerling, 1998; Fricke et al., 1998; Kohn et al., 1998; Straight et al., 2004), and bulk samples of tooth enamel collected from fragmentary material may only record some of this variability. To help overcome this potential problem, multiple teeth were collected and analyzed from each locality. Such sampling of multiple bulk samples should capture the seasonal variability experienced by a single population (Clementz and Koch, 2001).

Carbon and oxygen isotope ratios of milligram-sized enamel and dentine samples were soaked for 24 h in 0.1 N acetate-buffer solution, rinsed four times in distilled water, and dried (Koch et al., 1997). Stable isotope ratios are reported as $\delta^{13}C$ and $\delta^{18}O$ values, where $\delta = (R_{sample}/R_{standard} - 1) * 1000‰$, and the standard is VPDB for carbon and VSMOW for oxygen. $\delta^{18}O$ and $\delta^{13}C$ of tooth enamel carbonate were measured using an automated carbonate preparation device (KIEL-III) coupled to a Finnigan MAT 252 isotope ratio mass spectrometer at the University of Arizona and at the University of Iowa. Powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70 °C (UA) or 75 °C (UI) in the presence of silver foil. The isotope ratio measurement is calibrated based on repeated measurements of NBS-19, NBS-18 and in-house powdered carbonate standards. Analytical precision is ±0.1‰ for both $\delta^{18}O$ and $\delta^{13}C$ (1σ). The carbonate–CO_2 fractionation for the acid extraction is assumed to be identical to calcite.

Both isolated organic fragments and bulk sediment samples were soaked in 0.1 M HCl for 3 h, rinsed in distilled water four times, and dried. $\delta^{13}C$ was measured on a continuous-flow gas-ratio mass spectrometer (Finnigan Delta PlusXL). Samples were combusted using an elemental analyzer (Costech) coupled to the mass spectrometer. Standardization is based on NBS-22 and USGS-24. Precision is better than ±0.06 for $\delta^{13}C$ (1σ), based on repeated internal standards.

Carbon and oxygen isotope data for hadrosaur tooth enamel and dentine, gar scale ganoine and dentine, and invertebrate aragonite are given in Table 1. Stable isotope data for sedimentary organic material and paleosol carbonates are presented in Table 2.

Statistical comparisons of variance between sample populations were made using a simple *F*-test, and the appropriate student *t*-test was then used to compare mean values for sample populations. Statistical analyses were conducted using Microsoft Excel. Carbon and oxygen isotopic comparisons were made: (1) between enamel/ganoine and dentine from the same type of animal at each locality, and (2) between enamel and ganoine from coexisting hadrosaurs and gar at each locality. Results are summarized in Table 3.

6. Discussion

6.1. Diagenesis

6.1.1. Invertebrate aragonite remains

X-ray diffraction analysis of mollusc shells from the TMF and JRF indicates that these shells are composed of aragonite. Biogenic aragonite is a very unstable mineral, and after the death of the

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Table 1
Carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope data for hadrosaur enamel, gar scale ganoine, hadrosaur dentine, gar scale 'dentine', and TMF paleosol carbonates

Two Medicine	Gar-ganoine	δ13X	δ18O	Gar-dentine	δ13X	δ18O
	TM 2 M2GAR 1E	−4.1	19.6			
	HGAR 1	−4.5	17.6	TM 020 MGAR 2D	−3.6	19.6
	HGAR 2	−3.7	17.9	TM 020 MGAR 3D	−3.1	18.3
	HGAR 3	−3.2	18.1	TM 2 M2GAR 1D	−4.6	20.5
	MGAR 1	−3.6	17.9	TM 4 HSH HGAR 2D	−1.4	21.6
	MGAR 2	−5.4	16.3	TM 4 HSH HGAR 3D	0.9	23.3
	MGAR 3	−3.4	17.0	TM 4 HSH HGAR D	1.5	24.2
Average		−4.0	17.8		−1.7	21.3
st. dev.		0.7	1.0		2.5	2.2
Judith River	Gar-ganoine	δ13X	δ18O	Gar-dentine	δ13X	δ18O
	8303 Gar 1	1.6	19.4			
	8303 Gar 2	−2.5	20.5			
	8303 Gar 3	2.2	21.8			
	8303 Gar 5	1.0	20.7			
	8303 Gar 6	−0.1	19.4	8303 GAR1D	6.4	27.0
	8303 Gar 7	−0.9	20.1	8303 GR2D	8.7	30.9
	8303 GAR4E	1.3	22.1	8303 GR3D	10.8	32.9
	8303 GR10E	0.0	23.0	8303 GR6D	7.8	29.0
	8303 GR11E	1.0	20.9	8303 GR7D	10.7	30.4
	8303 G4E	1.8	21.8	8303 GR8D	7.1	26.8
	8303 G2E	−0.2	23.1	8303 GR4D	8.6	30.3
	8303 G3E	1.6	21.5	8303 GR10D	9.2	30.8
	8303 G1E	−1.3	22.0	8303 GR11D	9.6	29.6
Average		0.4	1.4		8.8	29.7
st. dev.		21.3	1.2		1.5	1.9
Dinosaur Park	Gar-ganoine	δ13X	δ18O	Gar-dentine	δ13X	δ18O
	ALBMATT G1E (2000)	−2.5	18.7			
	ALBMATT G2E	−1.7	20.4			
	ALBMATT G3E	−1.3	19.9			
	ALBMATT G4E	−3.0	20.1			
	ALBMATT G5E	−1.5	20.1	ALBMATT G1D (2000)	−0.1	19.3
	ALBMMBB G1E	0.3	21.0	ALBMATT G2D	−0.4	20.3
	ALBMMBB G2E	−0.3	19.0	ALBMATT G3D	−0.5	19.1
	ALBMMBB G3E	1.2	21.0	ALBMATT G4D	−0.7	20.2
	ALBMBB G4E	−2.3	20.7	ALBMATT G5D	−0.6	19.9
	ALBMMBB G5E	−0.8	20.4	ALBMMBB G1D	1.9	24.7
	ALBMMBB G6E	−2.2	19.6	ALBMMBB G2D	2.5	22.5
	ALBMMBB G7E	−3.0	18.6	ALBMBB G4D	3.4	22.6
Average		−1.4	20.0		0.7	21.1
st. dev.		1.3	0.8		1.6	2.0
Two Medicine	Hadro-enamel	δ13X	δ18O	Hadro-dentine	δ13X	δ18O
	HHA E	−6.2	17.9			
	HHB E	−6.0	19.6	HHA D	−4.5	19.8
	HHC E	−6.6	18.7	HHB D	−3.4	20.7
	HHD E	−5.6	18.8	HHC D	0.7	25.7
	HHE E	−5.9	21.5	HHD D	−0.4	22.8
	HHF E	−6.8	20.0	HHE D	−5.3	19.2
	HHG E	−7.7	19.7	HHF D	−6.9	18.3
	HHI E	−7.5	17.2	HHH D	−3.7	20.3
	TM053 H1	−7.0	18.2	HHI D	−4.6	19.5
	TM020 H1	−4.8	20.0	TMH1 D	−1.9	20.6
	TM020 H2	−6.6	19.3	tm053-H1D	−4.9	19.4
	TM H1	−6.9	18.8	tm020-H2D	10.9	37.0
	TM053 H2	−6.5	17.9	TM053 H4D	−2.1	20.9
	TM053 H4	−6.4	18.4	TM053 H4D	−0.2	22.4
	TM053 H5	−5.0	20.0	TM053 H5D	7.3	29.3
	TM053 H6	−6.0	19.6	TM053 H6D	0.0	23.6
	M2HE A	−5.7	18.3	M2HD A	−0.5	18.4
	M2HE B	−5.2	17.3	M2HD B	−6.5	17.9
	M2HE C	−6.2	20.2	M2HD C	−3.4	19.5
	M2HE D	−5.8	18.7	M2HD D	−2.8	18.9
Average		−6.2	19.0		−1.7	21.8
st. dev.		0.8	1.1		4.4	4.6
Judith River	Hadro-enamel	δ13X	δ18O	Hadro-dentine	δ13X	δ18O
	8303-02 H1E	−5.1	20.8			
	8303-02 H2E	−2.9	21.1			
	8303-02 H3E	−0.2	22.1			
	8303-02 H4E	0.3	23.0			
	8303-03 H1E	−2.8	19.9	8303-02 H1D	−0.1	22.3
	8303-03 H2E	−2.7	22.4	8303-02 H2D	3.9	21.6
	8303 H1E	−3.5	22.3	8303-02 H3D	6.5	23.7
	8303 H2E	−3.7	24.0	8303-02 H4D	2.8	20.5
	8303 H3E	−4.4	24.2	8303-03 H1D	5.1	22.3
	8303 H4E	−4.9	23.5	8303-03 H2D	4.0	20.8
Average		−3.0	22.3		3.7	21.9
st. dev.		1.8	1.4		2.2	1.2
Dinosaur Park	Hadro-enamel	δ13X	δ18O	Hadro-dentine	δ13X	δ18O
	ALB MATT H1E	−2.4	20.0	ALB MATT H1D	2.7	21.2
	ALB MATT H2E	−4.1	19.2	ALB MATT H2D	3.4	24.2
	ALB MATT H4E	−2.5	19.6	ALB MATT H4D	7.3	28.4
	ALB MATT H5E	−3.1	19.7	ALB MATT H5D	3.2	20.6
	ALB MATT H3E	−2.6	20.7	ALB MATT H3D	3.7	19.5
	ALBMATT H6E	−4.6	21.2	ALBMATT H1D	0.3	21.0
	ALBMATT H7E	−5.6	20.9	ALBMATT H2D	−1.0	20.0
	ALBMATT H8E	−2.3	20.5	ALBMATT H3D	3.0	21.6
	ALBMATT H9E	−3.9	20.7	ALBMATT H4D	1.2	19.9
	ALBMBB H1E	−1.9	22.1	ALBMBB H1D	4.6	22.1
	ALBMBB H2E	−4.7	18.7	ALBMBB H2D	2.1	21.7
	ALBMBB H3E	−3.4	19.3	ALBMBB H3D	−0.8	24.7
	ALBMBB H4E	−2.3	18.9	ALBMBB H4D	1.9	21.7
	ALBMBB H5E	−4.6	22.0	ALBMBB H5D	0.2	23.4
	ALBMBB H6E	−3.4	21.0	ALBMBB H6D	2.7	21.7
	ALBMBB H7E	−4.3	20.8	ALBMBB H7D	0.4	18.8
Average		−3.5	20.3		2.2	21.9
st. dev.		1.1	1.0		2.1	2.4
Two Medicine	Invert-aragonite	δ13X	δ18O			
	M2 BV1	−3.0	20.9			
	8303 BV4	−5.5	22.8			
	8303 BV5	−4.0	21.9			
Two Medicine	Paleosol carbonate	δ13X	δ18O			
	TM N2	−8.0	21.7			
	TM N3	−8.1	20.7			
	TM N4	−8.0	21.1			
	TM N5	−8.1	20.7			
	TM N6	−7.5	21.0			
	TM N7	−7.6	19.6			
	TM N8	−7.3	20.1			
	TM N9	−7.8	20.4			
	TM N10	−7.8	20.8			
	TM N11	−8.0	20.6			
	TM N12	−8.1	20.0			
	TM N13	−8.1	20.4			
Average		−7.9	20.6			
st. dev.		0.3	0.6			

Standard deviations are 1σ.

organism it will recrystallize to form calcite even at moderate temperatures and pressures. Thus, its occurrence in terrestrial sediments is in and of itself a strong indicator that these systems have not undergone intensive diagenetic alteration. In their study of Late Cretaceous unionid bivalves from the nearby Powder River basin, Dettman and Lohmann (2000) also commonly observe aragonite, and used its presence in part to argue that primary isotopic information was retained in shell material.

6.1.2. Comparisons of authigenic and tooth enamel carbonate

The rationale behind comparing isotope data from tooth enamel carbonate and paleosol carbonate is that authigenic minerals found in

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Table 2
Carbon ($\delta^{13}C$) isotope data from bulk sedimentary organic matter collected from Two Medicine and Judith River microfossil bonebeds

Two Medicine	Bulk	%C	δ13X
	TMO 1	3.7	−27.2
	TMO 2	4.2	−27.1
	TMO 3	4.0	−27.1
	TMO 4	1.1	−26.5
	TMO 5	0.9	−26.1
	TMO 6	1.0	−25.8
	TMO 7	3.0	−25.1
	TMO 8	2.4	−25.0
	TMO 9	3.6	−24.5
	TMO 10	1.0	−22.5
	TMO 11	4.0	−15.6
	TMO 12	5.8	−13.3
	H A	0.2	−25.7
	H B	0.3	−25.4
	H C	0.3	−25.4
	H E	0.3	−23.4
	H F	0.2	−26.3
	H G	0.3	−25.1
	H H	0.5	−25.1
	H I	0.3	−24.1
	H J	0.3	−25.8
	H K	0.5	−26.7
	H L	0.4	−26.6
	M B	1.8	−25.2
	M C	0.2	−26.9
	M D	0.2	−26.1
	M I	0.5	−25.9
	M J	1.3	−27.3
	M K	0.5	−25.6
	M L	1.0	−25.2
	M M	3.4	−24.7
	O C		−23.2
	O D		−23.5
	O E		−23.6
	O F		−23.5
	O G		−23.6
	O H		−22.8
	O I		−23.4
	O J		−23.8
	O K		−21.5
	O L		−24.8
Average			−24.5
st. dev.			2.7
Judith River	**Bulk**	**%C**	**δ13X**
	8303 E 03E 1		−24.6
	8303A 03A1		−25.4
	8303A 03A2		−25.0
	8303B 03B1		−25.4
	8303B 03B2		−25.4
	8303C 03C1		−24.4
	8303C 03C2		−25.1
	8303A 03AA		−24.9
	8303A 03AB		−23.9
	8303B 03B A		−24.2
	8303B 03B B		−23.9
	8303C 03 C B		−25.2
	8303C 03C A		−24.1
	8303E 03 E A		−24.4
	8303E 03 E A		−24.4
Average			−24.7
st. dev.			0.5

sediments hosting vertebrate remains should have isotope ratios that reflect those of diagenetic fluids and temperatures. Thus, any evidence of an isotopic relation between datasets, such as the formation of an isotopic mixing relationship or isotopic overlap can be used to identify effects of diagenetic overprinting of primary isotope ratios, whereas lack of mixing trends indicate that alteration is minimal (e.g. Quade et al., 1992; Barrick et al., 1996). As an example, tooth enamel carbonates from TMF hadrosaurs have higher $\delta^{13}C$ and lower $\delta^{18}O$ than associated paleosol carbonates and there is little overlap of data (Fig. 2). This lack of an isotopic relationship between materials can be used to argue that diagenetic overprinting of tooth enamel isotope ratios was not extensive, and that primary isotopic information is preserved in fossil material.

Although this isotopic comparison is consistent with enamel preserving primary isotopic information, it is difficult to determine if the timing of authigenic mineral formation, and the geochemical conditions reflected by authigenesis, are in fact the same as any diagenetic processes that may be affecting isotope ratios of bioapatite. In other words, authigenic mineral formation and isotopic alteration may be geochemically decoupled, as are processes of rare earth element alteration and isotope alteration (Trueman and Tuross, 2002). Furthermore, other than paleosol carbonates no other secondary carbonates were observed from the TMF, and carbonates of any kind are notably absent from the both the JRF and DPF. Thus this approach cannot be applied universally.

6.1.3. Tooth enamel and dentine carbonate

A similar, but geochemically more direct, comparison can be made for isotope data from related skeletal components, specifically enamel and dentine from the same tooth (e.g. Wang and Cerling, 1994; Stanton-Thomas and Carlson, 2003). Here, the rationale is (1) that these materials *are* affected by the same geochemical conditions at the same time, and (2) any isotopic differences between enamel, dentine, or bone reflects differences in crystal size and porosity, and hence susceptibility of these materials to isotopic exchange and precipitation of secondary minerals during diagenesis.

Table 3
Statistical comparisons of isotopic data sets (variable 1 and variable 2)

Variable 1	Variable 2	Test	*P* value	Significant?
TM gar, ganoine, carbon	TM gar, dentine, carbon	*t*-test unequal	0.040	No
TM gar, ganoine, oxygen	TM gar, dentine, oxygen	*t*-test unequal	0.005	Yes
TM hadro, enamel, carbon	TM hadro, dentine, carbon	*t*-test unequal	$P<0.001$	Yes
TM hadro, enamel, oxygen	TM hadro, dentine, oxygen	*t*-test unequal	0.008	Yes
TM hadro, enamel, oxygen	TM gar, ganoine, oxygen	*t*-test equal	$P<0.001$	Yes
TM hadro, enamel, carbon	TM hadro, ganoine, carbon	*t*-test equal	0.025	Yes
JR gar, ganoine, carbon	JR gar, dentine, carbon	*t*-test equal	$P<0.001$	Yes
JR gar, ganoine, oxygen	JR gar, dentine, oxygen	*t*-test equal	$P<0.001$	Yes
JR hadro, enamel, carbon	JR hadro, dentine, carbon	*t*-test equal	$P<0.001$	Yes
JR hadro, enamel, oxygen	JR hadro, dentine, oxygen	*t*-test equal	0.270	No
JR hadro, enamel, oxygen	JR gar, ganoine, oxygen	*t*-test equal	0.033	No
JR hadro, enamel, carbon	JR hadro, ganoine, carbon	*t*-test equal	$P<0.001$	Yes
DP gar, ganoine, carbon	DP gar, dentine, carbon	*t*-test equal	0.002	Yes
DP gar, ganoine, oxygen	DP gar, dentine, oxygen	*t*-test equal	0.030	No
DP hadro, enamel, carbon	DP hadro, dentine, carbon	*t*-test unequal	$P<0.001$	Yes
DP hadro, enamel, oxygen	DP hadro, dentine, oxygen	*t*-test unequal	0.002	Yes
DP hadro, enamel, oxygen	DP gar, ganoine, oxygen	*t*-test equal	0.001	Yes
DP hadro, enamel, carbon	DP hadro, ganoine, carbon	*t*-test equal	0.108	No

Comparisons of variance were made between groups using a simple *F*-test (not shown), and then the student *t*-test appropriate for equal or unequal variances was used to compare means among the data sets. *P*-values for these comparisons are given, and when $P<0.025$ the means are considered to be significantly different from each other.

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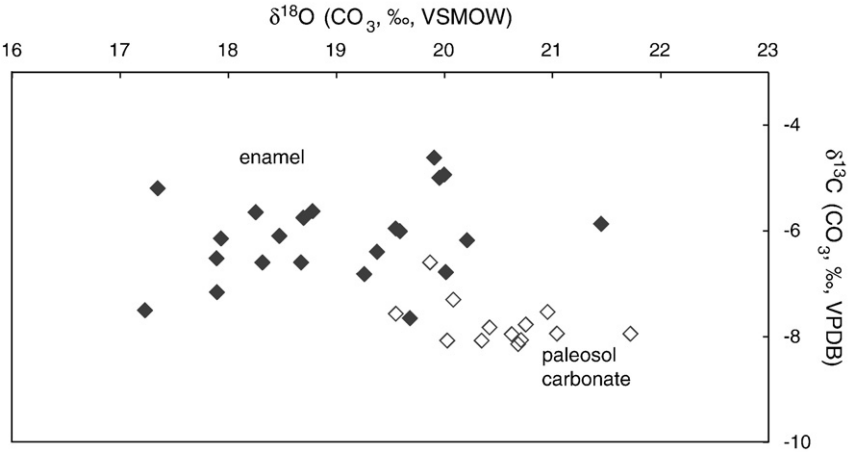

Fig. 2. Comparison of isotope data from tooth enamel and paleosol carbonate . Enamel samples are from Two Medicine hadrosaurs. Limited overlap and a lack of a linear mixing relationship between datasets are not consistent with diagenetic alteration of tooth enamel carbonate.

Oxygen and carbon isotope variability in enamel for a population of hadrosaurs (1σ = 1.0 to 1.4‰ for oxygen and 0.8 to 1.8‰ for carbon) is similar to that for populations of modern and ancient terrestrial mammals (Bocherens et al., 1996; Clementz et al., 2003, 2006; Feranec and MacFadden, 2006). In contrast, dentine is characterized by much more isotopic variability, (1σ = 1.2 to 4.6‰ for oxygen and 2.2 to 4.4‰ for carbon), and generally higher oxygen and carbon isotope ratios (Fig. 3). Similar isotopic relations between enamel and dentine have been also observed for hadrosaur remains of somewhat younger age in eastern Montana (Stanton-Thomas and Carlson, 2003).

The similarity in isotopic variability between hadrosaurs and terrestrial mammals suggests that diagenetic processes were not been pervasive enough to modify original ranges in $\delta^{18}O$ and $\delta^{13}C$. Thus any isotopic alteration of enamel values must be minimal. Increased isotopic variability and higher ratios for dentine, however, indicate that this more porous material has been subject to greater degrees of isotopic exchange and/or mineral infilling than enamel, although this isotopic modification is not uniform in nature. We suggest that the high isotope ratios associated diagenetic processes reflect concentrated microbial activity in dentine. As noted above, ^{12}C is preferred in many such reactions and is then removed from the system (Herczeg, 1988; Hornibrook et al., 2000), leaving more ^{13}C to interact with dentine. High oxygen isotope ratios may be higher due to the breakdown of organic matter and incorporation of some oxygen from it into pore waters and gases.

6.1.4. Comparison of tooth enamel carbonate among taxa

The third piece of evidence that supports the contention that interpretable primary carbon and oxygen isotope information is retained in enamel is provided by a comparison of stable isotope data from different taxa collected from the same microfossil bonebed. Such differences in the mean and variance for populations of different animals have been observed for modern taxa (Bocherens et al., 1996; Clementz et al., 2003; Sponheimer et al., 2003), and for fossil taxa from different time periods and localities (Feranec and MacFadden, 2000; Clementz et al., 2003; Cerling et al., 2004; Kohn et al., 2005; Botha et al., 2005; Feranec and MacFadden, 2006), and are expected if the animals in question are characterized by different physiologies and/or ecological behaviors. Isotopic offsets for enamel among animals would *not* be predicted to occur if isotopic alteration was extensive, as isotopic exchange with ground waters or secondary precipitation of apatite during diagenesis conditions should result in uniform isotope ratios for all remains in a single microfossil bonebed, regardless of taxonomic affinity.

As an example of this approach, $\delta^{13}C$ and $\delta^{18}O$ of associated hadrosaur teeth and gar scale ganoine were compared for the TMF, JRF, and DPF. In the case of the TMF and JRF, data are also included from aragonitic invertebrate shells. For each formation, statistically significant differences in mean carbon isotope ratios are observed between hadrosaurs and gar, while smaller offsets in oxygen isotope ratios also occur (Table 3). Differences in $\delta^{13}C$ and $\delta^{18}O$ between vertebrates and aragonitic invertebrates are also observed. Equally important, the direction of offsets between site-specific hadrosaur-gar pairs are generally the same in all three localities, *regardless of absolute isotope ratio*, with gar scales having lower $\delta^{18}O$ and higher $\delta^{13}C$ relative to hadrosaurs (Fig. 4).

Because of this consistency regardless of location, the similar thicknesses of enamel and ganoine, and the similar mineralogy and structure of enamel and ganoine, these isotopic offsets between vertebrates are interpreted to reflect original taxonomic differences in physiology or behavior. In particular, the lower $\delta^{18}O$ value of ~28‰ at the present time, does not play a major role in their oxygen budget, while it does for terrestrial vertebrates. It is also possible that river water ingested by fish has a lower $\delta^{18}O$ influenced by runoff from high-elevation source areas (e.g. Dettman and Lohmann, 2000; Dutton et al., 2005), while hadrosaurs ingested more local meteoric water. Higher $\delta^{13}C$ values for fish probably reflect differences in biogeochemical processes that take place as carbon is incorporated into bioapatite, and/or variable sources of carbon in freshwater systems. The former is poorly studied, but it is known that weathering of marine carbonate sedimentary rocks, input of carbon from multiple organic sources, and interactions with the atmosphere can all result in $\delta^{13}C$ values of dissolved carbon that are much higher than those for terrestrial plants (e.g. Boutton, 1991).

In summation, several lines of evidence indicate that diagenetic overprinting of primary isotopic ratios in enamel and ganoine is limited. These include (1) the preservation of biogenic aragonite in the TMF and JRF, and the isotopic offset of this material relative to vertebrate remains, particularly from in the TMF, (2) ranges in $\delta^{18}O$ and $\delta^{13}C$ for hadrosaurs that are similar to those observed for terrestrial animals, and (3) consistent isotopic differences between fish ganoine and hadrosaur enamel from all three areas (TMF, JRF, DPF).

6.2. 'High' $\delta^{13}C$ and diet-enamel offsets for hadrosaurs

To this point, discussion of isotope data has focused on relative differences among material or animals. Here we address absolute $\delta^{13}C$ values for hadrosaurs. For recent, pre-industrial time periods, herbivorous mammals eating plants from an average C_3 ecosystem are predicted to have $\delta^{13}C$ values that range from −18 to −8‰ (MacFadden and Cerling, 1996). These values and their range reflect (1) average $\delta^{13}C$ of C_3 plants which are in turn influenced by $\delta^{13}C$ of atmospheric CO_2, (2) isotopic variability of C_3 plants due to local environmental conditions and/or plant type, and (3) an average offset between $\delta^{13}C$

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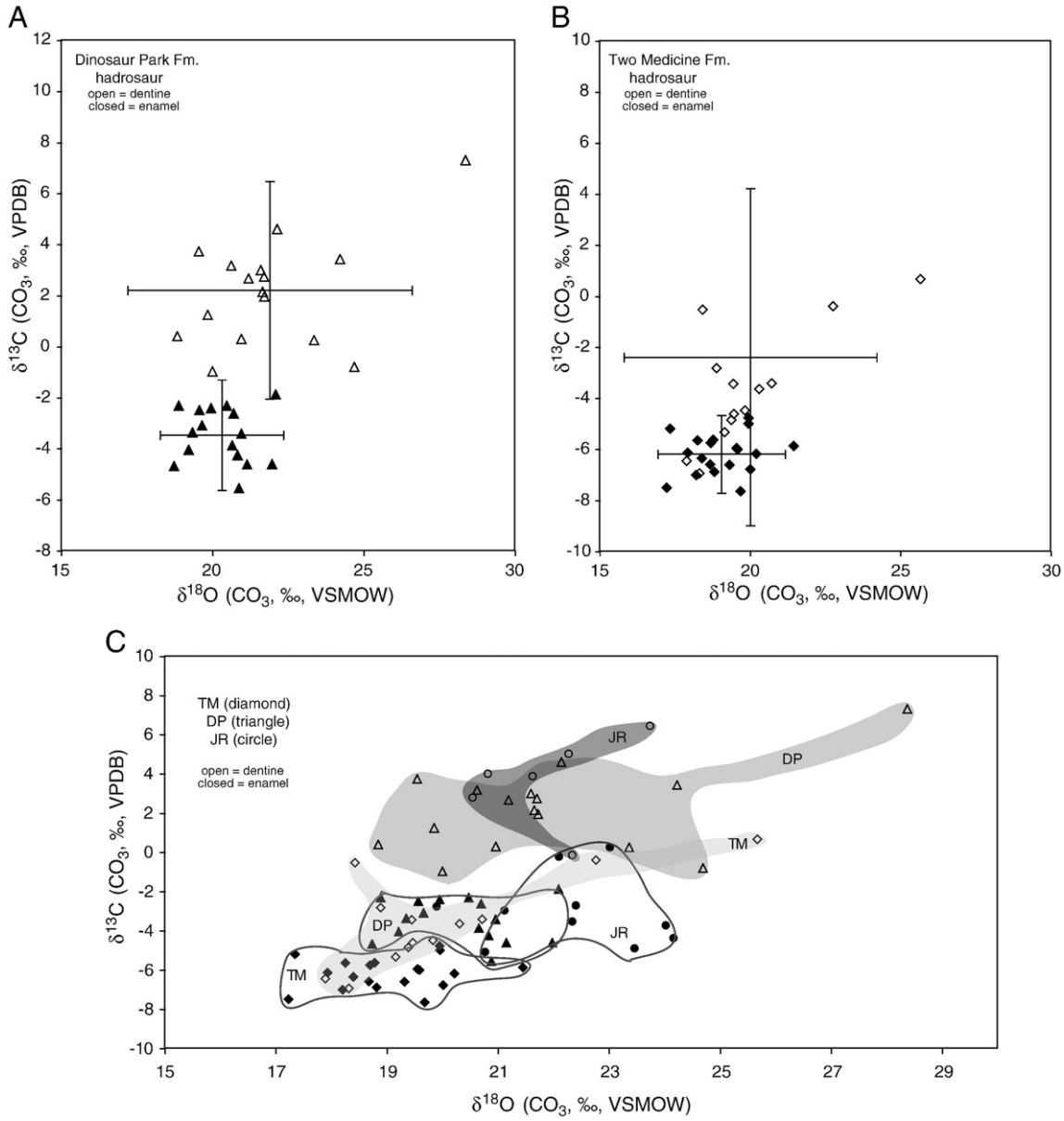

Fig. 3. Comparisons of isotope data from hadrosaur tooth enamel and dentine of the same tooth (averages ±2σ). (A) Hadrosaur teeth from the Dinosaur Park Formation, (B) hadrosaur teeth from the Two Medicine Formation, (C) all hadrosaur enamel and dentine data. In all cases, dentine is characterized by higher carbon and oxygen isotope ratios and by greater isotopic variability. These results are consistent with isotope ratios of dentine having been affected to a larger degree by diagenetic processes, and indicate that carbonate from enamel is more likely to have preserved primary isotopic information.

of bioapatite and that of bulk diet of 14‰. Mean $\delta^{13}C$ values of hadrosaurs from the TMF, DPF and JRF, however, are −6.3‰ and −3.4 and −3‰, respectively, much higher than expected for mammals occupying a C_3 ecosystem.

Stanton-Thomas and Carlson (2003) observed similar relatively 'high' $\delta^{13}C$ values in their study of Late Cretaceous hadrosaurs, and they suggested several reasons for them, including: (1) diagenetic alteration, (2) a diet comprised of significant amounts of plants with a C_4 or CAM photosynthetic pathway, (3) higher $\delta^{13}C$ of atmospheric CO_2 during the Late Cretaceous compared to the present day, (4) a diet comprised of plants with higher than average $\delta^{13}C$, whether they be plants experiencing water stress or gymnosperms that typically have $\delta^{13}C$ higher than other associated plant taxa, and (5) a carbon isotope offset between diet and tooth enamel carbonate ($\Delta\delta^{13}C_{diet\text{-}enamel}$) that is larger than that for modern mammals.

Of these possibilities, diagenetic alteration of enamel is an unlikely candidate, as there is little evidence for extensive modification of isotope ratios based on the isotopic comparisons presented above. Similarly, a hadrosaur diet comprised almost exclusively of C_4 or CAM plants is also unlikely because there is no other evidence to suggest that these types of plants were present in large abundance in these Late Cretaceous ecosystems (e.g. Cerling, 1999). In contrast, there is evidence that $\delta^{13}C$ of atmospheric CO_2 was higher during the Late Cretaceous, and that as a result the average $\delta^{13}C$ of a C_3 ecosystem may have been 1–2‰ higher at that time (Barrera and Savin, 1999; Hasegawa et al., 2003). Carbon isotope data from sedimentary organic matter from TMF and JRF localities support the possibility that hadrosaurs were eating plants with a $\delta^{13}C$ higher than the present, as average values are −24.7 and −24.5‰ respectively. Furthermore $\delta^{13}C$ values of organic matter up to ~−21‰ are observed (Table 3), indicating that plants with higher than average $\delta^{13}C$ were present.

Despite these considerations, it is still difficult to account for $\delta^{13}C$ values higher than ~−6‰ as long as it is assumed that hadrosaurs had a $\Delta\delta^{13}C_{diet\text{-}enamel}$ of 14‰. It is not unreasonable, however, to believe

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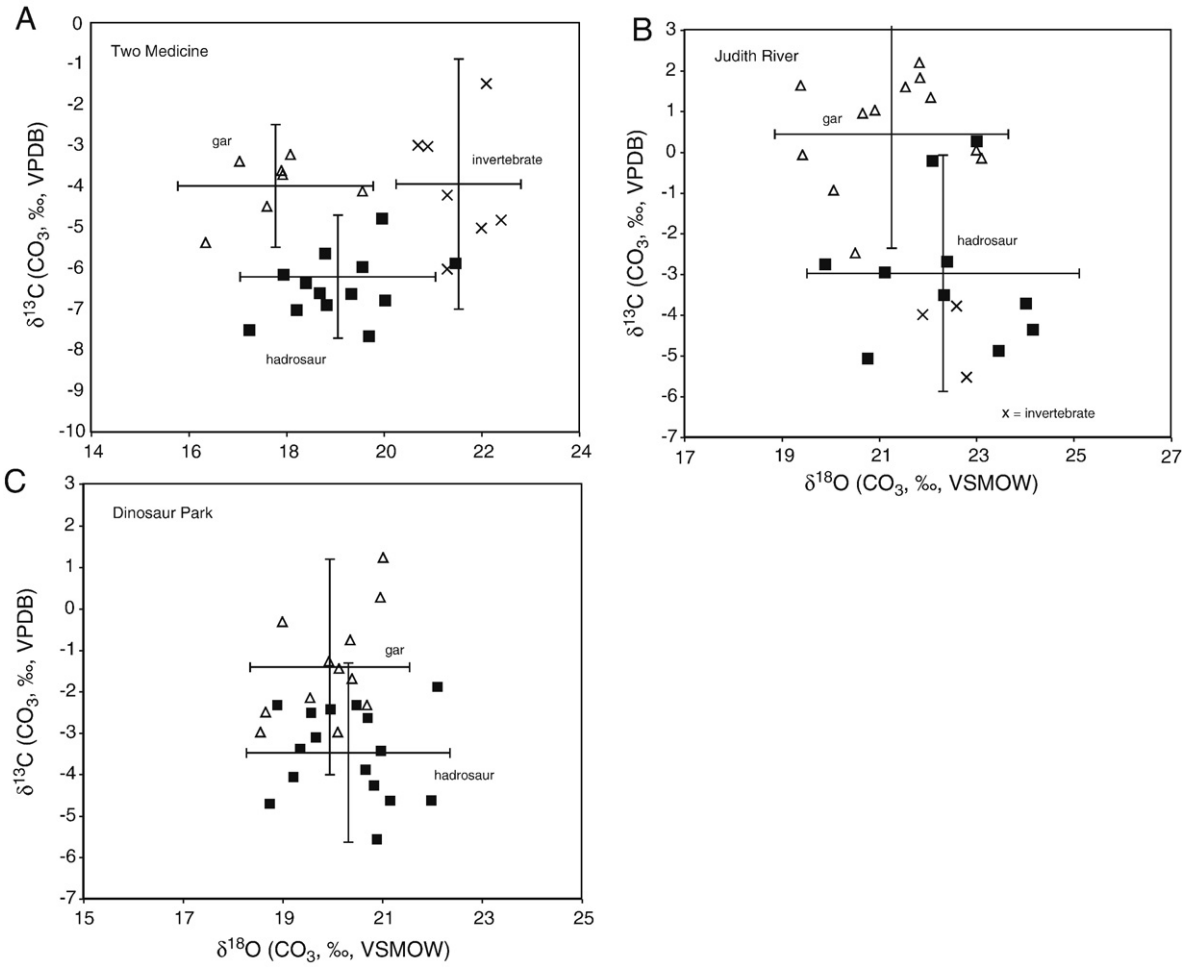

Fig. 4. Isotopic differences between enamel and ganoine from coexisting hadrosaurs and gars, respectively (averages ±2σ). Samples from (A) the Two Medicine Formation, (B) Judith River Formation, and (C) Dinosaur Park Formation all exhibit similar isotopic relations between taxa, with gar having higher carbon isotope ratios and lower oxygen isotope ratios. In the case of the TMF and JRF, data from invertebrate aragonite are shown with an '×'. These offsets are interpreted to represent original behavioral and physiological differences (see text). Extensive overprinting of primary isotope signals by diagenetic carbonate should result in uniform isotope ratios. Thus, the occurrence of taxonomic differences is evidence that complete isotopic resetting did not occur.

that this offset may have been larger for hadrosaurs, perhaps closer to 18‰, thus making it possible to account for average hadrosaur $\delta^{13}C$ values of −2‰. For one, $\Delta\delta^{13}C_{diet\text{-}enamel}$ is in fact variable for large mammalian herbivores, ranging from ~12 to 15‰ (Koch, 1998; Cerling and Harris, 1999; Kohn and Cerling, 2002; Hoppe et al., 2004; Passey et al., 2005). Birds are closer taxonomic relatives to hadrosaurian dinosaurs than are mammals, and although not directly analogous to tooth enamel carbonate, the offset between $\delta^{13}C$ of eggshell carbonate and bulk diet for large birds are even greater (~16‰; Johnson et al., 1998). Reasons for variations in $\Delta\delta^{13}C_{diet\text{-}enamel}$ are thought to reflect taxonomic differences in (1) the biogeochemical processes that take place as carbon from plants is incorporated into bioapatite, particularly methane production during digestion, and/or (2) which organic compounds in a plant (i.e. proteins, carbohydrates, lipids) are actually utilized by the animal when forming bioapatite (Gannes et al., 1998; Hedges, 2003; Jim et al; 2004; Passey et al., 2005). Thus it is possible that hadrosaurs utilized organic compounds in ways different than herbivorous mammals and birds, or produced a larger percentage of methane in their stomachs during longer rumination periods, and these factors lead to a larger $\Delta\delta^{13}C_{diet\text{-}enamel}$.

Indirect evidence that indicates that $\Delta\delta^{13}C_{diet\text{-}enamel}$ was higher for hadrosaurs is found by comparing $\delta^{13}C$ of hadrosaur tooth enamel and $\delta^{13}C$ of paleosol carbonate. Carbon is soil carbonates forming more than ~30 cm below the surface has a source in respired plant material, but these carbonates have $\delta^{13}C$ values ~14 to 17‰ higher than these plants due to the effects of CO_2 diffusion in soils and on temperature (Cerling et al., 1991). In the case of the TMF, $\delta^{13}C$ of hadrosaur tooth enamel is still higher than associated paleosol carbonate nodules by another ~2‰ (Fig. 2). The implication is that carbon isotope ratios of hadrosaur tooth enamel were offset to higher values relative to local plants by ~16 to 19‰, depending on the effects of CO_2 diffusion and temperature on $\delta^{13}C$ of paleosol carbonate at that time.

Other indirect evidence indicating that $\Delta\delta^{13}C_{diet\text{-}enamel}$ was higher for hadrosaurs is found by comparing $\delta^{13}C$ of hadrosaur tooth enamel and $\delta^{13}C$ of sedimentary organic matter from the same localities. Considering the TMF and JRF together, the average offset is ~18‰ higher than those of associated organic material (Fig. 5A). This type of comparison can be expanded to include material from 10 other microfossil bonebeds ranging in age from late Campanian to late Maastrichtian and in space from western Montana to western North Dakota (Fig. 5B; Fricke, unpublished data), and an average offset in $\delta^{13}C$ between hadrosaur tooth enamel and sedimentary organic matter of ~18‰ is still observed. There are obvious limitations to this approach, in that (1) $\delta^{13}C$ of bulk organic matter preserved in sediment may not be representative of the average $\delta^{13}C$ that actually existed on the surface during the Late Cretaceous, and (2) hadrosaurs in these may have had dietary preferences for specific plants areas, and thus did not eat them all in equal abundance. Nevertheless, the remarkable consistency of this isotopic offset gives credence to the

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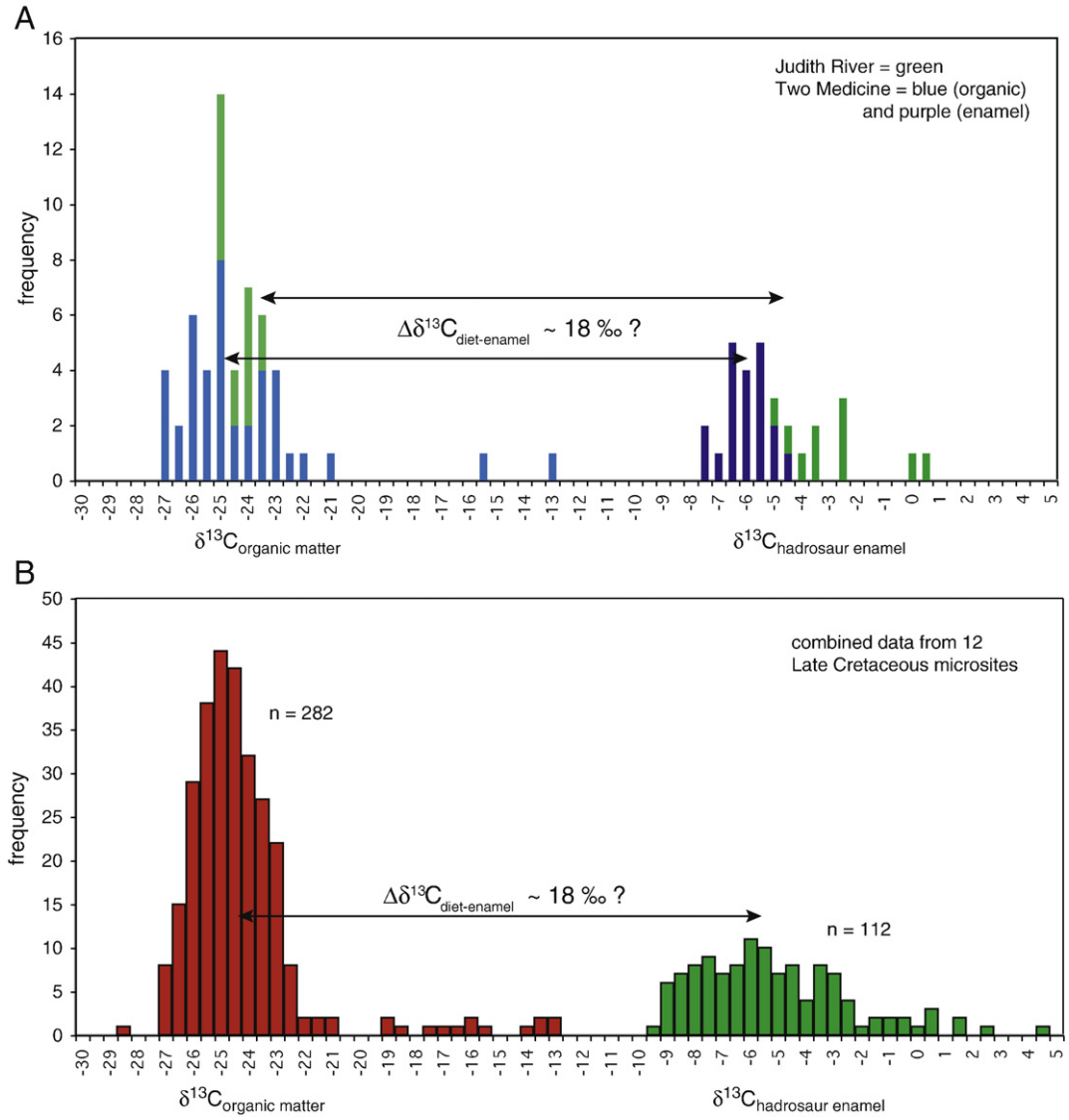

Fig. 5. (A) $\delta^{13}C$ of hadrosaur tooth enamel and $\delta^{13}C$ of bulk sedimentary organic matter collected from microfossil bonebeds in the Two Medicine Formation and Judith River Formations. The range in $\delta^{13}C$ of TMF-JRF organic matter is similar to modern C_3 plants, although absolute values are several per mil higher than modern values due in part to higher $\delta^{13}C$ of atmospheric CO_2 during the Late Cretaceous. The average offset for both areas is ~18‰. (B) Carbon isotope data from coexisting bulk sedimentary organic matter and charcoal and hadrosaurian tooth enamel from a total of 12 microfossil bonebeds in the Judith River Formation ($n=2$), the Two Medicine Formation ($n=1$), the Hell Creek Formation of North Dakota ($n=8$) and the Lance Formation of Wyoming ($n=1$). Isotope data are normally distributed, as observed for modern C_3 grasses and mammalian herbivores (e.g. Cerling et al., 1997); the only difference is the larger average offset of ~18‰. This offset exists regardless of exact age, location, depositional environment, or hadrosaur species, and this is consistent with a true biological signal.

idea that hadrosaurs, like their closest modern relatives (i.e. birds), had a larger $\Delta\delta^{13}C_{diet\text{-}enamel}$ than modern herbivorous mammals.

6.3. Late Cretaceous environments

The isotopic comparisons presented above provide reasonable evidence that primary isotopic information has not been totally obscured by diagenetic processes, and thus can be used to study environments of the past. Interpretations of these data will be aided by considering the sedimentological and taphonomic context in which fossil remains were found. Furthermore, interpretations will be aided by comparing carbon and oxygen isotope data from the different formations in order to reconstruct isotopic gradients and to compare isotopic variability. For example, a comparison of all carbon and oxygen isotope data makes it clear that there is an overall decrease in $\delta^{13}C$ and $\delta^{18}O$ from coastal lowland localities of the JRF and DPF to inland and upland localities of the TMF, and that intra-populational variations in isotope ratios are larger for the coastal sites (Fig. 6). By focusing on relative differences in isotope ratios from place to place, it is possible to hypothesize potential underlying factors that may have caused these differences.

Before doing so, it is important to reiterate that different hadrosaur species are found in different formations (see Fig. 1 caption), and in theory physiological differences between them may be the source of some of the isotopic differences observed from place to place. We do not think, however, that hadrosaur physiology is a factor because (1) the normal distribution of carbon isotope ratios for hadrosaurs from 12 different microfossil bonebeds (Fig. 5) indicates that no species-level differences in $\Delta\delta^{13}C_{diet\text{-}enamel}$ exist, and (2) empirical relations between oxygen isotope ratios of bioapatite and those of meteoric water for extant vertebrates are remarkably constant regardless of taxonomic level.

6.3.1. Coastal–inland gradients: carbon

Focusing first on carbon isotope data from hadrosaurian tooth enamel, average ratios for the coastal JRF and DPF are similar, while

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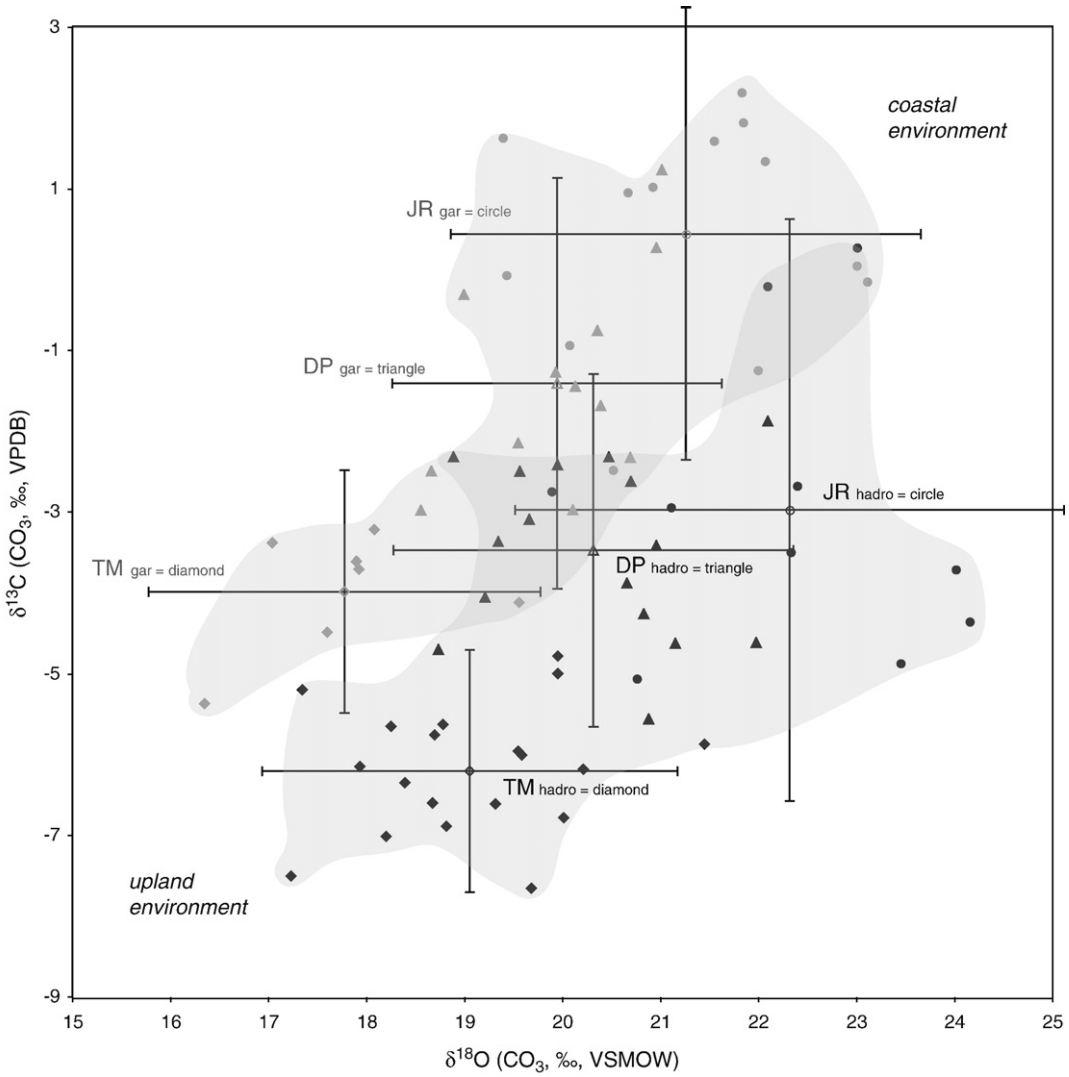

Fig. 6. Major trends in all carbon and oxygen isotope data from hadrosaur enamel and gar scale ganoine (averages in open symbols, $\pm 2\sigma$ for samples from each formation). Higher isotope ratios are associated with the lowland coastal plain sediments of the Dinosaur Park and Judith River Formations, while lower isotope ratios are characteristic of the inland and upland Two Medicine Formation.

ratios for the upland TMF are ~3‰ lower, while the intra-populational variability of the TMF is about half that of the more coastal JRF (as expressed by the standard deviation; Fig. 6). At the most basic level, these differences in carbon isotope ratios should reflect differences in the types of plants ingested by hadrosaurs in these geographically distinct areas, or in the environmental conditions influencing plant growth.

Based on these considerations, along with knowledge of the overall sedimentological context of the different fossil-bearing localities (Fig. 1), carbon isotope data from hadrosaurs can be interpreted to represent a change in environmental conditions and vegetation structure across a Late Cretaceous paleolandscape. In particular, higher and more variable $\delta^{13}C$ near the coast indicates that plants living in these areas were subjected to environmental conditions different and perhaps more varied than those living in upland areas. These isotopic characteristics are likely due to reduced stomatal conductance of CO_2 as plants reacted to a number of different microenvironmental factors such as osmotic stress associated with brackish waters of the near shore, nutrient stress associated with water logged and poorly developed soils, or evaporative water stress associated with open, sun-baked settings, all of which are consistent with sedimentological reconstructions of the JRF and DPF (Rogers, 1998; Eberth, 2005). In contrast, lower $\delta^{13}C$ values from the TMF are consistent with areas of closed vegetation located on river floodplains. In such areas, plants would have access to nutrient-rich soils, they would not suffer extensive water loss due to evaporation or exposure to salt water, and they may have even utilized recycled carbon under a forest canopy. It is also tempting to speculate that upland environments of the TMF were more uniform spatially (i.e., the mosaic of distinct paleoenvironments was perhaps more limited), which in turn could account for the smaller amount of carbon isotope variability observed for the TMF.

Isotopic studies of ancient and modern ecosystems provide some support for these suggested links between depositional environments and carbon isotope systematics. In their study of Cenomanian terrestrial plant remains, Nguyen Tu et al. (1999) observed a range in $\delta^{13}C$ values from −23 to −28‰, where different plant types were characterized by different average $\delta^{13}C$. Based on sedimentology and on the ecological preferences of modern relatives, they concluded that these plants occupied a variety of coastal microenvironments characterized by different salinities. In a similar study of early Cretaceous leaves, Aucour et al. (2008) observed a ~7‰ range in $\delta^{13}C$ of cuticle from conifers that were inferred to have lived under variable environmental conditions. At the present time, investigations of a single kind of C_3 plant from the coastal swamp setting of Belize (red mangrove tree, *Rhizophora mangle*) demonstrate that their

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average $\delta^{13}C$ values can vary from ~−24 to ~−28‰ depending on tree size, water salinity, nutrient availability, and other possible factors (McKee et al., 2002; Wooller et al., 2003). Furthermore, intra-site variability in $\delta^{13}C$ for this single species is ~1.8‰ (±1σ; Wooller et al., 2003). In contrast to these coastal settings, modern tropical forests from Puerto Rico and Brazil are characterized by lower average $\delta^{13}C$ values that range from −26.9 to −32.1‰ (von Fischer and Tieszen, 1995; Martinelli et al., 1998). For individual plant species, and even whole forests, variability in $\delta^{13}C$ is lower than for coastal mangroves, on the order of 0.2 to 1.5‰ (±1σ; von Fischer and Tieszen, 1995; Martinelli et al., 1998).

Carbon isotope data from gar scales have an overall gradient similar to that of hadrosaurs (Fig. 6), however $\delta^{13}C$ of gar from the JRF are higher than those from Dinosaur Park, even though $\delta^{13}C$ of hadrosaurs are similar between these areas. This difference likely reflects a change in the source of carbon that is utilized by fish in these areas. While carbon from decaying C_3 plant material is likely to be a major component of the carbon budget in river waters of all areas, it is possible that ocean water is mixing with river water, particularly in Judith River settings that are more proximal to the coast. Dissolved carbon in ocean water typically has much higher $\delta^{13}C$ than fresh water (Boutton, 1991), and studies of fish otiliths from the Cretaceous Interior Sea indicate that $\delta^{13}C$ ranged from 0 to +2‰ (Carpenter et al., 2003). Therefore only a small amount of fresh water–ocean water mixing in near coastal waters could account for higher $\delta^{13}C$ of gar from the JRF.

6.3.2. Coastal–inland gradients: oxygen

Oxygen isotope gradients and variability are slightly different than that of carbon. In particular, average isotope ratios from hadrosaurian tooth enamel decrease *regularly* by ~3.3‰ as distance from the Cretaceous Inland Seaway increases (Fig. 6). Furthermore, oxygen isotope variability of all hadrosaur populations is approximately the same (as expressed by the standard deviation; Table 1). Assuming that $\delta^{18}O$ of hadrosaur tooth enamel is reflecting that of ingested surface water, these patterns can be used to study hydrological conditions of the region during the Late Cretaceous.

The decrease in $\delta^{18}O$ of 3.3‰ over a 300–400 km transect from east to west (Fig. 1) most likely reflects the progressive rainout of moisture from air masses. One possible cause of atmospheric cooling and hence rainout is the 'continentality effect', which occurs as air masses move progressively from ocean over land at relatively low elevations (Rozanski et al., 1993). The average gradient in $\delta^{18}O$ with distance at the present time, however, is only ~2‰/1000 km for low-elevation sites (Rozanski et al., 1993; Araguas-Araguas et al., 1998), thus other factors must be causing $\delta^{18}O$ to decrease. One possibility is elevation change from JRF to TMF regions. Rainout of air masses occurs as elevation increases so that $\delta^{18}O$ decreases ~2.8‰/1 km elevation change in the case of precipitation (Poage and Chamberlain, 2002), and $\delta^{18}O$ decreases ~4.2‰/1 km elevation change in the case of river water (Dutton et al., 2005). Another factor is the removal of large amounts of moisture from air masses during large convective storm events. Even in the absence of large elevation changes, $\delta^{18}O$ can decrease by ~1.4‰/100 cm of rainfall (i.e. the 'amount effect').

To explain the east to west decrease in $\delta^{18}O$, and the likely involvement of elevation changes and/or storm events, we hypothesize that this coastal region (Fig. 1) was characterized by a monsoonal atmospheric circulation pattern during the Late Cretaceous. In particular, warming of high-elevation areas to the west of the TMF that formed during the Sevier orogeny resulted in low atmospheric pressures during the summer, and this in turn drew moisture inland (i.e. east to west) off of the Cretaceous Interior Sea. Rainout and isotopic distillation of this moisture then occurred due to a relatively large increase in elevation, or due to rapid rainout from monsoonal storm systems. Although this scenario is difficult to confirm at present, global climate model simulations for earlier Cretaceous time periods indicate that air did move inland from the seaway during the summer months (Poulsen et al., 1999).

While east to west rainout of air masses is thought to play the dominant role in producing the $\delta^{18}O$ patterns observed for hadrosaur tooth enamel, it is possible that other variables were also playing a role. For example, in this study rocks of the DPF are interpreted to have been deposited in a coastal plain setting inland of the JRF. Yet $\delta^{18}O$ of Dinosaur Park hadrosaurs are ~2.1‰ lower than those of the Judith River. One possible explanation for this incongruity is that Dinosaur Park sites are located at higher latitudes than those of the Judith River, and that a decrease in $\delta^{18}O$ with latitude (of ~0.27‰/° latitude; Rozanski et al., 1993) is superimposed on the east–west trend described above.

The regional pattern in $\delta^{18}O$ obtained from gar scales parallels that observed for hadrosaurs, and is thus consistent with the movement and rain out of air masses moving from east to west. Isotope data from gar, however, can also be used to estimate the actual $\delta^{18}O$ of river water during the late Cretaceous in these areas. Such estimates are possible because $\delta^{18}O$ of fish hard parts are influenced by both $\delta^{18}O$ of river water and by temperatures of river water (Kolodny et al., 1983; Patterson et al., 1993). Therefore by using a reasonable range in possible temperatures along with the calcite–water fractionation equation (Kim and O'Neil, 1997), it is possible to estimate $\delta^{18}O$ of the river water in these regions. Doing so for temperatures of 15 to 30 °C results in estimated average $\delta^{18}O$ of river water from the TMF of −9.2 to −12.2‰, for the DPF of −7 to −10‰ and for the JRF of −5.7 to −8.7‰, assuming that carbonate in ganoine undergoes isotopic fractionation in a manner similar to inorganic calcite.

In their study of bivalve aragonite from southern Alberta, Dettman and Lohmann (2000) estimated that $\delta^{18}O$ of river water ranged from −14 to −19‰ during the late Campanian. They interpreted these low values to reflect runoff from snowmelt in high-elevation areas to the west that flow through lowland areas to the east with minimal isotopic 'dilution' by local lowland precipitation. Considered in this context, higher $\delta^{18}O$ of gar sampled here are more indicative of rivers having a source in more local, lower elevation precipitation. It is also possible that these river waters were shifted to higher isotope ratios due recharge by groundwater that was subject to evaporation in the vadose zone. In either case, estimated $\delta^{18}O$ values of river indicate that the ecosystems being sampled as part of this study were associated with smaller tributaries rather than major trunk rivers.

7. Summary

A major goal of this paper is to demonstrate that the word 'Mesozoic' needs not be a "stop sign" when it comes to using stable isotope methods to study biology of extinct animals and environments of the past. We contend that while it is difficult to say unambiguously that no diagenetic alteration of material this age has occurred, it *is* possible to argue that diagenesis has not eliminated all primary stable isotope information. We do so here by noting that (1) biogenic aragonite with isotope ratios distinct from those of vertebrates is preserved, (2) isotope ratios of tooth enamel carbonate are distinct from paleosol carbonate from the same sediments, (3) tooth enamel has lower and less variable isotope ratios compared to dentine from the same tooth, and (4) consistent isotopic differences exist among different taxa, in particular hadrosaurs and gar, regardless of location.

In light of these results, interpretations are made regarding dinosaur biology and paleoenvironmental conditions. For example, the occurrence of 'high' $\delta^{13}C$ values for hadrosaur tooth enamel relative to modern mammals is interpreted to reflect a larger carbon isotope offset between diet and tooth enamel for hadrosaur dinosaurs relative to modern mammals. Indirect evidence supporting this contention is found by comparing $\delta^{13}C$ of hadrosaur tooth enamel with $\delta^{13}C$ of associated plants remains and paleosol carbonates. A

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potential implication of the larger $\delta^{13}C_{diet\text{-}enamel}$ offset in hadrosaurs is that they utilized organic compounds in a different way than modern mammals. It is tempting to speculate that gut biology, particularly as it relates to methane production and rumination times, differed between hadrosaurs and modern mammalian herbivores.

Finally, the decrease in $\delta^{13}C$ observed from the coastal plain facies of the JRF and DPF to the upland facies of the TMF is hypothesized to reflect a change in the type and variety of environmental factors influencing C_3 plants in these paleogeographically distinct regions, in particular the availability of salt and fresh water and nutrients, and the density of vegetation. $\delta^{18}O$ is also observed to decrease from the JRF to the TMF, and this is presumed to reflect the rainout of air masses moving inland from the Cretaceous Interior Seaway. The oxygen and carbon isotope gradients documented herein using dinosaur and fish bioapatite illustrate the utility of comparing isotope data derived from multiple microfossil bonebeds across a well-documented ancient landscape, and arguably provide a robust means of tracking environments and climates in pre-Cenozoic deposits.

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