

Hadrosaurid migration: inferences based on stable isotope comparisons among Late Cretaceous dinosaur localities

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Abstract.—Stable carbon and oxygen isotope ratios were measured for carbonate in samples of hadrosaurid tooth enamel and dentine, and gar scale ganoine and dentine from five geologically “contemporaneous” (two-million-year resolution) and geographically distant late Campanian formations (Two Medicine, Dinosaur Park, Judith River, Kaiparowits, and Fruitland) in the Western Interior Basin. In all cases, isotopic offsets were observed between enamel and dentine from the same teeth, with dentine being characterized by higher and more variable carbon and oxygen isotope ratios. Isotopic offsets were also observed between gar ganoine and hadrosaur enamel in all sites analyzed. Both of these observations indicate that diagenetic overprinting of enamel isotope ratios did not entirely obfuscate primary signals. Decreases in carbon and oxygen isotope ratios were observed in hadrosaur enamel from east to west, and overlap in isotope ratios occurred only between two of the sampled sites (Dinosaur Park and Judith River Formations).

The lack of isotopic overlap for enamel among localities could be due to diagenetic resetting of isotope ratios such that they reflect local groundwater effects rather than primary biogenic inputs. However, the large range in carbon isotope ratios, the consistent taxonomic offsets for enamel/ganoine data, and comparisons of enamel-dentine data from the same teeth all suggest that diagenesis is not the lone driver of the signal. In the absence of major alteration, the mostly likely explanation for the isotopic patterns observed is that hadrosaurids from the targeted formations were eating plants and drinking waters with distinct isotopic ratios. One implication of this reconstruction is that hadrosaurids in the Late Cretaceous of the Western Interior did not migrate to an extent that would obscure local isotopic signatures.

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Accepted: 2 December 2008

Introduction

The emerging view of the Dinosauria paints a picture of fast-growing, large-bodied vertebrates with far-reaching geographic distributions that undoubtedly required abundant resources. Exactly how dinosaurs procured vital resources on a regular basis remains somewhat controversial, especially given the occurrence of members of the group in high-latitude localities where seasonal fluctuations in both temperature and light availability would presumably have been significant (Clemens and Allison 1985; Davies 1987; Brouwers et al. 1987; Fiorillo and Gangloff 2001). Did dinosaurs possess physiological traits and practice ecological strategies that made it possible for them to remain in place and thrive on a year-round basis, or did they instead migrate with the seasons as many animals do today? In their efforts to address the likelihood of long-range dinosaur migration, paleobiologists

have struggled with several controversial aspects of dinosaur thermoregulation and behavior (e.g., Hotton 1980; Parrish et al. 1987; Currie 1989; Clemens and Nelms 1993; Fiorillo and Gangloff 2001; Bell and Snively 2008), and the issue arguably remains unresolved.

On a more local scale, researchers have argued fairly convincingly for distinct provincialism among dinosaurs, most notably in the western interior of North America (e.g., Lehman 1987, 1997, 2001). These paleobiogeographic studies are based primarily upon previously published data sets that reveal patterns in the spatial distributions and facies associations of dinosaur remains. For example, Lehman (2001) reviewed dinosaur distribution data in roughly 5-Myr bins during the Campanian and Maastrichtian, and concluded that there was marked endemism in western North America among the large herbivorous dinosaurs, specifically the ceratopsians and

hadrosaurs. This indication of provincialism was explained in the context of distinct forage preferences and narrow environmental tolerances.

In this paper we take a different approach to address questions of dinosaur migration and provincialism, one that uses stable isotope ratios of fossil tooth enamel as a record of ingested food and water resources. In general, comparisons of isotopic data from contemporaneous fossil remains collected in different regions can reveal whether animals shared the same resources, and thus occupied the same areas. Through a series of such comparisons, patterns of movement of extinct animals can be constrained. As part of this study, hadrosaur fossils were analyzed from a suite of well-known formations in the Western Interior Basin of North America that range geographically from northern New Mexico to southern Alberta, and all fall within an approximately 2-Myr time interval of the Late Cretaceous. By comparing isotopic data from these localities, it is possible to test two major sets of hypotheses regarding hadrosaurian movement during this time period: east-west migration, as has been suggested for nesting behavior, and north-south migration, as has been suggested for polar dinosaurs.

This study is significant because stable isotope methods are independent of a priori assumptions that relate to dinosaur physiology and behavior. Moreover, our data set is arguably stable in a taxonomic sense, because we focus on hadrosaurs at the family level and do not attempt to distinguish subfamilies (hadrosaurines versus lambeosaurines), genera, or species. Results suggest that hadrosaurids did not migrate to an extent that would obscure local isotopic signatures linked to food and water resources. This result is consistent with previous paleobiogeographic reconstructions that indicate that hadrosaur dinosaurs had limited geographic ranges.

Stable Isotope Ratios and Migration

The purpose of this section is to explain in more detail how comparisons of stable isotope data collected in different regions can shed light on whether animals shared the same resources, and thus can provide constraints on

patterns of movement. The stable isotope approach takes advantage of the fact that carbon isotope ratios of C3 plants, which made up Mesozoic ecosystems, change in response to environmental conditions (e.g., O'Leary 1988; Farquhar et al. 1989; O'Leary et al. 1992; Kohn and Cerling 2002). Likewise, 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 hydrological mixing and the rain-out "history" of air masses that are supplying precipitation to these surface water reservoirs (e.g., Epstein and Mayeda 1953; Dansgaard 1964; Rozanski et al. 1993; Gat 1996). As a result a mosaic of isotopic domains can exist over any given landscape (Fig. 1).

Animals record the isotopic characteristics of their host isotopic domains when they ingest organic material and drink from surface water reservoirs and then form bioapatite [$\text{Ca}_5(\text{PO}_4)_3(\text{OH}, \text{CO}_3)$], which is a major component of tooth enamel, tooth dentine, bone, and body scales. Carbon found in the carbonate phase of bioapatite is related to ingested organic material, such as plants in the case of herbivores (Koch et al. 1994; Koch 1998; Cerling and Harris 1999; Passey et al. 2005), and carbon isotope ratios are influenced by which organic compounds are ingested and how they are utilized during metabolic processes (DeNiro and Epstein 1978; Gannes et al. 1998; Hedges 2003; Jim et al. 2004; Passey et al. 2005). Oxygen in vertebrate bioapatite is derived primarily from ingested water and atmospheric oxygen, sources 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 $\sim 23\text{‰}$ (Kohn 1996). Thus, it probably does not influence oxygen isotope *variations* in bioapatite of vertebrates living in different places or drinking different waters.

Because bioapatite provides a record of the isotopic domains occupied by an animal, isotopic comparisons among populations can be used to address questions of migration. To illustrate this approach, carbon and oxygen iso-

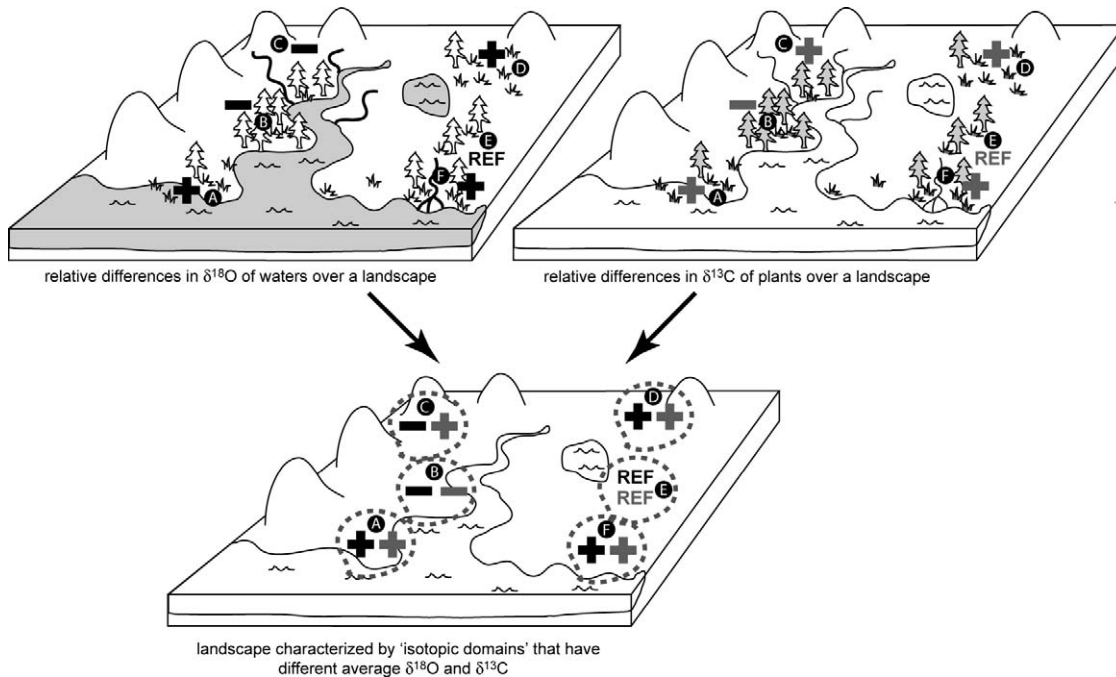


FIGURE 1. Schematic illustration of how different parts of a single C3 ecosystem can be characterized by distinct isotopic domains (after Fricke 2007). These areas include coastal freshwater swamps (A), riparian forest canopy (B), streams with precipitation from high elevation (C), open shrubland (D), mixed forest/shrubland (E), and zone of marine and freshwater mixing (F). Using area E as a baseline (REF), plants living in areas A, C, D, and F are likely to have higher $\delta^{13}\text{C}$, whereas those living in areas B and C are likely to have lower $\delta^{13}\text{C}$. Reasons for relatively higher $\delta^{13}\text{C}$ values include slow rates of diffusion of CO_2 through water (A); lower concentrations of CO_2 in the atmosphere at higher elevations (C); enhanced aridity and thus less moisture availability in open environments (D); osmotic stress in brackish waters along with the possibility of evaporative tidal flat settings (F). Reasons for relatively lower $\delta^{13}\text{C}$ values include recycling of CO_2 in the understory of dense, closed-canopy forests, and the abundant availability of freshwater. Using area E as a baseline, water from A, D, and F are likely to have higher $\delta^{18}\text{O}$, whereas that from B and C is likely to have lower $\delta^{18}\text{O}$. Reasons for relatively higher $\delta^{18}\text{O}$ values include evaporation of standing water, particularly in open vegetation or arid settings (A); enhanced evaporation of leaf water in sunnier, windier open settings (D); mixing of high $\delta^{18}\text{O}$ ocean water with freshwater sourced in precipitation (F). Reasons for relatively lower $\delta^{18}\text{O}$ values include reduced evaporation of leaf water in humid, shady and still understory settings (B); collection of precipitation from higher elevations having lower $\delta^{18}\text{O}$ values (C).

tope data for modern populations of bison living in restricted areas over a swath of the western United States (Hoppe 2006; Hoppe et al. 2006) can be considered (Fig. 2). Significant differences in carbon or oxygen isotope ratios reflect isotopic differences in the proportion of C3 versus C4 grasses in their diet, and a latitudinal decrease in oxygen isotope ratios of surface water they drank, respectively. More importantly, this lack of isotopic overlap reflects their non-migratory behavior. Hoppe (2004) used similar kinds of isotopic comparisons of mammoth tooth enamel to conclude that these animals from the Great Plains did not undertake large migrations of over 600 km but instead migrated distances of several hundred kilometers or less. This approach is not

without uncertainties, however, as isotopic overlap for two populations of a single taxon found in separate areas could indicate that each population consumed plants and water with isotope ratios that happened to be similar to one other. This is the case for bison populations from Theodore Roosevelt National Park, Ordway Prairie Preserve, Badlands National Park, and Wind Cave National Park (Fig. 2).

Nature of the Cretaceous Sample

The conceptual basis for the current study outlined above is fairly straightforward when considering modern materials. When dealing with fossil remains, however, issues of dinosaur taxonomy and paleobiology and strati-

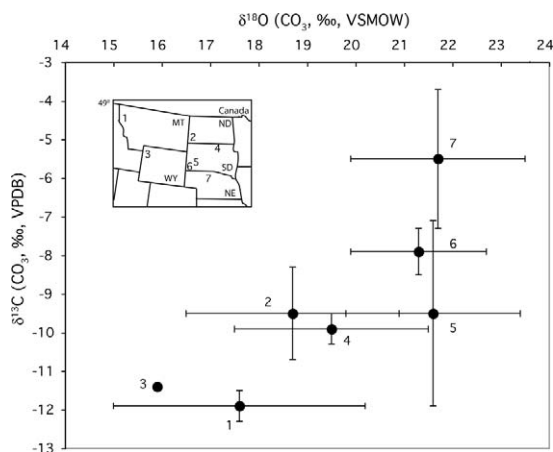


FIGURE 2. Carbon and oxygen isotope data from modern populations of bison living over a swath of western North America. Data and location map are from Hoppe (2006) and Hoppe et al. (2006). Isotopic differences among these non-migratory populations reflect differences in carbon isotope ratios and oxygen isotope ratios of ingested food and water, respectively. The occurrence of similar kinds of offsets for ancient herbivores can be used to infer similar non-migratory behavior.

graphic correlation need to be considered. We believe that we have taken the necessary steps to address these issues and identify a sample suitable for this type of study.

Sampling Strategy and Taxonomic Considerations.—This study focuses on the isotopic analysis of hadrosaurid teeth (both intact specimens and fragments), ganoid gar scales, and invertebrate shell fragments recovered via surface collection and screening. It is not possible to identify teeth beyond the family level (Hadrosauridae), and therefore it is possible that teeth from multiple species within this major group were analyzed together (Table 1). However, this lack of taxonomic reso-

lution has no bearing on our study, because we are testing whether the group as a whole shows geographically distinct or overlapping isotopic values during the 2-Myr study interval. Similarly, there was no attempt to identify ganoid fish scales beyond Lepisosteidae (referred to as “gar” in this paper).

From a taphonomic perspective, all of the vertebrate material analyzed was derived from microfossil bonebeds (sensu Eberth et al. 2007; Rogers and Kidwell 2007). These types of fossil accumulations, with their great abundance of disarticulated and dissociated skeletal material, are ideal for the comparative approach we followed, because each specimen can be assumed to represent a distinct individual unless association among elements can be demonstrated (Badgley 1986). Multiple teeth and scales were collected and analyzed from each study area in an effort to “capture” all the isotopic variability in carbon and oxygen isotope ratios of ingested plant matter and water that may have been occurred seasonally (Fricke and O’Neil 1996; Sharp and Cerling 1998; Fricke et al. 1998; Kohn et al. 1998; Straight et al. 2004). A statistical analysis by Clementz and Koch (2001) suggests that data from multiple “bulk” samples of enamel, such as those obtained from isolated/fragmentary teeth, are sufficient if they are assumed to represent a single population of animals.

A possible concern associated with using isotopic data from hadrosaurids to investigate migration is that, unlike mammals, they shed and replaced teeth throughout their lifetimes. Therefore, if rates of tooth growth and tooth replacement were on the order of weeks, a

TABLE 1. Approximate age of each microfossil bonebed and hadrosaurid taxa found at that stratigraphic level within each formation. Even though the exact identification of hadrosaurid taxa is not possible from isolated teeth, identifying those taxa known from particular stratigraphic levels allows more accurate representation of possible taxa within a particular bonebed. Faunal data are derived from published reports (Horner 1992; Sullivan and Williamson 1999; Williamson 2000; Horner et al. 2001; Horner et al. 2004; Gates and Evans 2005; Ryan and Evans 2005; Evans and Reisz 2007) and unpublished data from one of us (T.A.G.).

Formation	Site name	Age of site	Hadrosaurid taxon
Dinosaur Park	Millar’s Bonebed	ca. 75 Ma	<i>Lambeosaurus magnicristatus</i> , <i>Lambeosaurus lambei</i> , <i>Prosaurolophus maximus</i>
Judith River	UC-8303	ca. 75 Ma	<i>Gryposaurus</i> sp.?, <i>Brachylophosaurus canadensis</i>
Two Medicine	Land Slide Butte	ca. 75–74 Ma	<i>Maiasaura peeblesorum</i> , <i>Gryposaurus</i> sp., <i>Prosaurolophus blackfeetensis</i> , <i>Hypacrosaurus stebingeri</i>
Kaiparowits	UMNH VP Loc 108	75.4 Ma	<i>Gryposaurus</i> sp., <i>Parasaurolophus</i> sp.
Fruitland	NMMNH 4010	ca. 75.5–74.5 Ma	<i>Parasaurolophus cyrtocristatus</i> , <i>Hadrosaurinae</i> indet.

tooth on which enamel formed while an animal occupied one isotopic domain on a landscape may fall out before migration of that individual took it to a different area. Such a high tooth turnover rate could make the identification of multi-year (reproductive) migrations particularly problematic. Fortunately, estimates of the rate of tooth growth range from 183 to 339 days for the mineralization of an adult hadrosaurid tooth (Erickson 1996; Stanton-Thomas and Carlson 2004). Thus at any one time, the dental battery of an adult animal, made up of hundreds of teeth, would contain a multi-year isotopic history of food and water intake. This in turn suggests that if intra-annual (seasonal), and even extended, migrations of hadrosaurids took place we would expect to find isotopic overlap among areas because teeth forming in one isotopic domain could readily be transported to another before being shed.

Stratigraphic Correlation.—Fossil remains were collected from six localities that define east-west and north-south transects in the Western Interior Basin (Fig. 3). The sampled localities include (1) two microfossil bonebeds in the Two Medicine Formation (TMF) in northwestern western Montana, (2) one microfossil bonebed in the Judith River Formation (JRF) of north-central Montana, (3) one microfossil bonebed in the Dinosaur Park Formation (DPF) of southern Alberta, (4) one microfossil bonebed in the Kaiparowits Formation (KAF) of southern Utah, and (5) one microfossil bonebed in the Fruitland Formation (FRF) of New Mexico. Taken together, the six sampled sites span ~16 degrees in latitude (from ~36° to 52°) and ~5 degrees in longitude (from ~108° to 113°). All bonebeds included in this study can be confidently placed in the late Campanian (Ogg et al. 2004), and on the basis of associated radioisotopic data (Rogers et al. 1993; Eberth 2005; Eberth and Deino 2005; Roberts et al. 2005; Sullivan and Lucas 2006; Foreman et al. in press), constrained to an interval ranging from ca. 74.0 to 76.0 Ma. Marine isotope data indicate that carbon isotope ratios of oceans varied by only ~0.25‰ and temperature varied by only ~1–2°C during this time period (Barrera and Savin 1999), and for this reason we assume that

no major error is introduced by comparing isotopic data from sites of slightly different ages, and that these data can be combined to represent the late Campanian in general.

All localities occur in alluvial and coastal plain facies that accumulated in the Western Interior Basin, to the west of the Cretaceous Interior Seaway (Fig. 3). The two sampled sites in the TMF occur near the top of the formation, and are associated with fluvial and floodplain facies that represent deposits of the semiarid alluvial uplands (upland is used herein as indicative of being hundreds of kilometers distant from the coeval shoreline of the Cretaceous Interior Seaway) (Rogers 1990, 1994, 1998). The locality in the JRF is intercalated in facies that accumulated in a hydromorphic coastal setting, in close proximity to the advancing seaway (Rogers 1998). The locality in the correlative DPF also accumulated in a “lowland” coastal setting in paralic facies, although it appears to have been situated somewhat farther updip and more distant from contemporaneous shoreline facies than the nearby Judith River locality (Eberth and Hamblin 1993; Eberth 2005; D. Eberth personal communication 2007). The microfossil bonebed targeted in the KAF accumulated in a subhumid alluvial system characterized by abundant deposits of flood-basin ponds, large suspended-load channels, and poorly developed hydromorphic paleosols. Finally, the locality analyzed in the FRF lies within the Fossil Forest Member, ~10 m below the contact. It is associated with trough-crossbedded sandstones, drab colored silt and mudstones, and minor amounts of coal, all consistent with wet, fluvial-deltaic depositional environments (Lucas et al. 2006).

Methods and Results

Samples were taken for analysis by using a Dremel drill with diamond-tipped bits. 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 milligram-sized enamel and dentine samples were soaked for 24 hours 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 $\delta^{13}\text{C}$ and

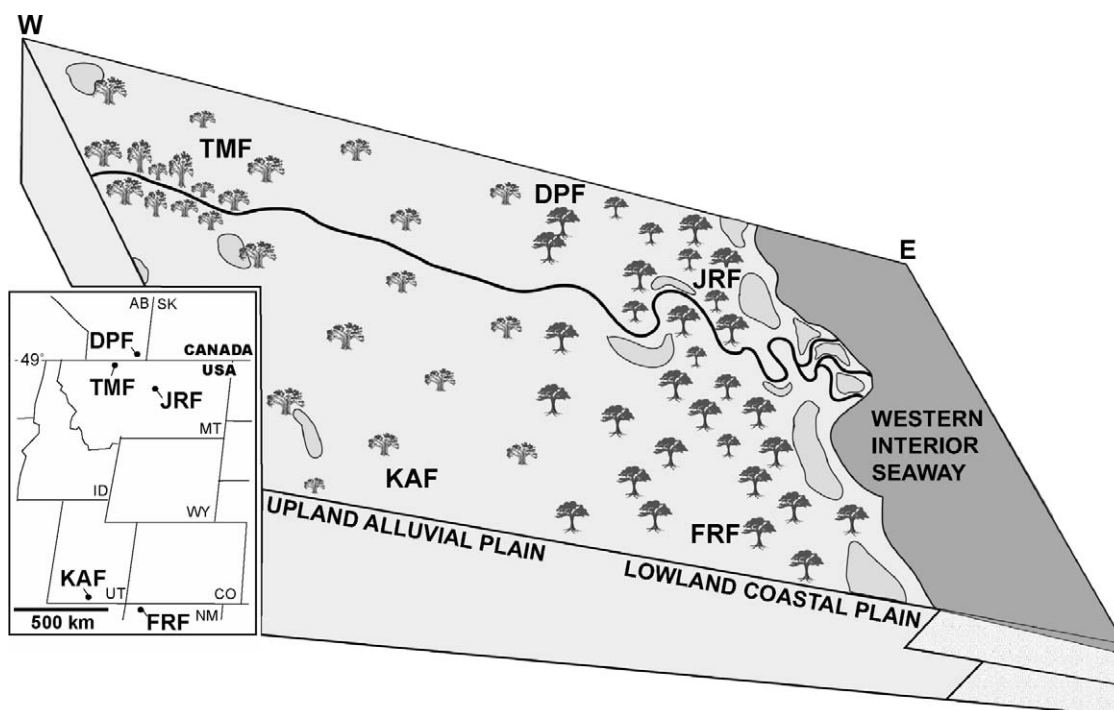


FIGURE 3. Schematic diagram illustrating relative paleogeographic positions of localities in the Two Medicine Formation (TMF, “alluvial uplands”), Judith River Formation (JRF, shoreline proximal coastal lowlands), Dinosaur Park Formation (DPF, “intermediate upper coastal plain”), Kaiparowits Formation (KAF, humid alluvial plain), and Fruitland Formation (FRF, coastal plain). Inset map illustrates geographic locations of sampled sites.

$\delta^{18}\text{O}$ values, where $\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) \cdot 1000\text{‰}$, and the standard is VPDB for carbon and VSMOW for oxygen. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of tooth enamel and shell carbonate were measured by using an automated carbonate preparation device (KIEL-III) coupled to a Finnegan 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 on the basis of repeated measurements of NBS-19, NBS-18, and in-house powdered carbonate standards. Analytical precision is $\pm 0.1\text{‰}$ for both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ (1σ). The carbonate $-\text{CO}_2$ fractionation for the acid extraction is assumed to be identical to calcite. Mineralogical composition of invertebrate shell material was analyzed with a Phillips 1710 X-ray diffractometer at Colorado College.

Carbon and oxygen isotope data for hadrosaurid tooth enamel and dentine, and gar

scale ganoine and dentine from the TMF, DPF, and JRF have been published previously (Fricke et al. 2008) and are summarized in Table 2. New isotope data for samples from the KAF and FRF are also given in Table 2. New isotopic data for bivalve samples are given in Table 3. Simple F -tests were used to determine whether two sample populations being compared had equal or unequal variances, and then the appropriate student t -test was used to compare mean values for these populations. Statistical analyses were conducted with Microsoft Excel. Carbon and oxygen isotopic comparisons were made (1) between enamel/ganoine and dentine from each locality, (2) between enamel and ganoine from coexisting hadrosaurids and gar at each locality, and (3) between enamel of hadrosaurs collected from different formation. Statistical analyses of previously published data (Fricke et al. 2008) along with the analyses of new isotopic data are summarized in Tables 4–6.

The most important observations obtained from these results are that (1) significant dif-

TABLE 2. Carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope data (SMOW) for hadrosaurid enamel, gar scale ganoin, hadrosaurid dentine, and gar scale "dentine." Standard deviations are 1σ .

Formation	Gar-ganoin			Gar-dentine			Hadrosaur-enamel			Hadrosaur-dentine		
	Sample	Carbon	Oxygen	Sample	Carbon	Oxygen	Sample	Carbon	Oxygen	Sample	Carbon	Oxygen
Dinosaur Park	$n = 12$	(-1.4, 1.3)	(20.0, 0.8)	$n = 8$	(0.7, 1.6)	(21.1, 2.0)	$n = 16$	(-3.5, 1.1)	(20.3, 1.0)	$n = 16$	(2.2, 2.1)	(21.9, 2.4)
Judith River	$n = 13$	(0.4, 1.4)	(21.3, 1.2)	$n = 9$	(8.8, 1.5)	(29.7, 1.9)	$n = 10$	(-3.0, 1.8)	(22.3, 1.4)	$n = 6$	(3.7, 2.2)	(21.9, 1.2)
Two Medicine	$n = 7$	(-4.0, 0.7)	(17.8, 1.0)	$n = 6$	(-1.7, 2.5)	(21.3, 2.2)	$n = 20$	(-6.2, 0.8)	(19.0, 1.1)	$n = 19$	(-1.7, 4.4)	(21.8, 4.6)
Fruitland	FRU G1E	-4.9	22.6	FRU G1D	-0.5	23.1	FRU H1E	-6.8	22.6	FRU H1D	-2.1	25.6
	FRU G2E	-4.2	21.7	FRU G2D	-0.4	21.3	FRU H2E	-6.5	23.0	FRU H2D	2.3	24.1
	FRU G3E	-5.7	21.6	FRU G3D	1.0	23.3	FRU H3E	-7.2	23.1	FRU H3D	-0.2	22.4
	FRU G4E	-4.3	21.6	FRU G4D	0.7	24.4	FRU H4E	-2.5	22.6	FRU H4D	3.8	25.4
	FRU G5E	-2.8	22.4	FRU G6D	-0.1	22.0	FRU H5E	-5.5	21.4	FRU H5D	3.0	25.9
	FRU G6E	-2.8	21.5	FRU G7D	0.3	23.7	FRU H6E	-7.3	22.0	FRU H6D	0.6	21.9
	FRU G7E	-4.3	21.5	FRU G8D	0.9	23.1	FRU H7E	-5.3	22.9	FRU H7D	1.4	25.7
	FRU G8E	-2.4	21.5	FRU G9D	0.4	26.9	FRU H8E	-7.0	22.2	FRU H8D	2.9	26.3
	FRU G10E	-4.1	21.1	FRU G10D	0.4	22.9		(-6.0, 1.6)	(22.5, 0.6)	FRU H9D	6.1	25.5
		(-3.9, 1.1)	(21.7, 0.5)		(0.3, 0.5)	(23.4, 1.6)					(2.0, 2.4)	(24.7, 1.6)
Kaiparowits	KAP G1E	-6.0	22.6				KAP H1E	-8.5	22.1	KAP H1D	-7.1	21.3
	KAP G2E	-5.0	22.2				KAP H2E	-8.3	21.2	KAP H2D	-5.0	22.6
	KAP G3E	-5.4	20.2				KAP H3E	-9.5	23.3	KAP H3D	-9.0	22.1
	KAP G4E	-6.4	22.8				KAP H4E	-7.5	21.5	KAP H4D	-6.3	21.9
	KAP G5E	-7.2	19.2				KAP H5E	-9.4	22.3	KAP H5D	-9.0	21.9
	KAP G6E	-7.2	20.3				KAP H6E	-9.0	21.8	KAP H6D	-7.4	22.0
	KAP G7E	-7.1	20.5				KAP H7E	-8.6	23.1	KAP H7D	-7.4	22.3
	KAP G8E	-7.3	22.1				KAP H8E	-8.7	22.9	KAP H8D	-6.0	22.0
	KAP G9E	-5.9	19.6				KAP H9E	-9.0	23.8	KAP H9D	-5.7	22.1
	KAP G10E	-7.7	21.5				KAP H10E	-9.3	21.0	KAP H10D	-7.9	20.7
		(-6.5, 0.9)	(21.1, 1.3)				KAP H11E	-8.1	22.5	KAP H11D	-6.9	22.2
							KAP H12E	-8.8	22.0	KAP H12D	-8.3	22.6
							KAP H13E	-7.6	23.5	KAP H13D	-4.3	23.0
							KAP H14E	-8.1	22.6	KAP H14D	-5.7	22.3
							KAP H15E	-9.1	21.8	KAP H15D	-8.5	22.3
								(-8.6, 0.6)	(22.4, 0.8)		(-7.0, 1.5)	(22.1, 0.5)

TABLE 3. Carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope data (SMOW) for bivalve aragonite. Standard deviations are 1σ .

Formation	Bivalve-aragonite		
	Sample	Carbon	Oxygen
Judith River	JR 8303 BV1	-3.8	22.6
	JR 8303 BV4	-5.5	22.8
	JR 8303 BV5	-4.0	21.9
Two Medicine	TM M2 BV1	-3.0	20.9
	TM M2 BV2	-1.5	22.1
	TM M2 BV3	-3.0	20.7
	TM M2 BV4	-6.0	21.3
	TM M2 BV5	-4.2	21.3
	TM M2 BV6	-5.0	22.0
	TM M2 BV7	-4.8	22.4
		(-3.9, 1.5)	(21.5, 0.6)
Fruitland	FRU BV1	-5.5	21.1
	FRU BV2	-5.8	21.4
	FRU BV3	-5.1	21.4
	FRU BV4	-7.1	24.2
	FRU BV5	-6.6	22.3
		(-6.0, 0.8)	(22.1, 1.3)

ferences in $\delta^{18}\text{O}$ and/or $\delta^{13}\text{C}$ occur between enamel/ganoine and dentine at each locality, (2) significant differences in $\delta^{18}\text{O}$ and/or $\delta^{13}\text{C}$ are observed among coexisting fish and dinosaur taxa from individual formations, and (3) significant differences in $\delta^{18}\text{O}$ and/or $\delta^{13}\text{C}$ are observed among hadrosaurids collected from different formations. In general, dentine

is characterized by higher $\delta^{13}\text{C}$ and to a lesser extent $\delta^{18}\text{O}$ values and by more isotopic variability relative to enamel/ganoine from the same teeth (Fig. 4). Gar typically have higher $\delta^{13}\text{C}$ and lower $\delta^{18}\text{O}$ values than hadrosaurids regardless of formation (Fig. 5). Hadrosaurid enamel samples from the inland and upland TMF and KAF localities are generally characterized by lower $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ relative to coastal areas. Although isotopic overlap among formations does occur, enamel and ganoine are significantly different from one another in either $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ in all cases (Fig. 6).

Discussion

Possible Reasons for Isotopic Differences

The goal of this study is to make comparisons of isotopic data from contemporaneous fossil remains collected in different regions in order to make inferences regarding patterns of hadrosaurid movement. To do so, it must first be determined if diagenesis, defined here as the chemical alteration of bioapatite after the death of an animal, obscured original behavioral information and is the cause of the observed offsets in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ among locations (Fig. 6). If not, then two other expla-

TABLE 4. Statistical comparisons of isotopic data from enamel/ganoine and associated dentine (variable 1 and variable 2). Simple F -tests were used to determine if two sample populations being compared had equal or unequal variances, and then the appropriate student t -test was used to compare mean values for sample populations. When $p < 0.05$, populations are considered to be significantly different from each other. Higher isotope ratios for dentine are suggestive of greater diagenetic alteration relative to enamel/ganoine. Results in italics were first published by Fricke et al. (2008).

Variable 1	Variable 2	p -value	Significant?
<i>JR gar, ganoine, carbon</i>	<i>JR gar, dentine, carbon</i>	0.00	yes
<i>JR gar, ganoine, oxygen</i>	<i>JR gar, dentine, oxygen</i>	0.00	yes
<i>JR hadro, enamel, carbon</i>	<i>JR hadro, dentine, carbon</i>	0.00	yes
<i>JR hadro, enamel, oxygen</i>	<i>JR hadro, dentine, oxygen</i>	0.27	no
<i>DP gar, ganoine, carbon</i>	<i>DP gar, dentine, carbon</i>	0.00	yes
<i>DP gar, ganoine, oxygen</i>	<i>DP gar, dentine, oxygen</i>	0.03	yes
<i>DP hadro, enamel, carbon</i>	<i>DP hadro, dentine, carbon</i>	0.00	yes
<i>DP hadro, enamel, oxygen</i>	<i>DP hadro, dentine, oxygen</i>	0.00	yes
<i>TM gar, ganoine, carbon</i>	<i>TM gar, dentine, carbon</i>	0.04	yes
<i>TM gar, ganoine, oxygen</i>	<i>TM gar, dentine, oxygen</i>	0.01	yes
<i>TM hadro, enamel, carbon</i>	<i>TM hadro, dentine, carbon</i>	0.00	yes
<i>TM hadro, enamel, oxygen</i>	<i>TM hadro, dentine, oxygen</i>	0.01	yes
<i>KA hadro, enamel, carbon</i>	<i>KA hadro, dentine, carbon</i>	0.00	yes
<i>KA hadro, enamel, oxygen</i>	<i>KA hadro, dentine, oxygen</i>	0.32	no
<i>FR gar, ganoine, carbon</i>	<i>FR gar, dentine, carbon</i>	0.00	yes
<i>FR gar, ganoine, oxygen</i>	<i>FR gar, dentine, oxygen</i>	0.01	yes
<i>FR hadro, enamel, carbon</i>	<i>FR hadro, dentine, carbon</i>	0.00	yes
<i>FR hadro, enamel, oxygen</i>	<i>FR hadro, dentine, oxygen</i>	0.00	yes

TABLE 5. Statistical comparisons of isotopic data from enamel/ganoine/aragonite *among taxa* from the same formation (variable 1 and variable 2). See Table 4 for statistical tests used. When $p < 0.05$, populations are considered to be significantly different from each other. The occurrence of significant isotopic differences among hadrosaurids indicates that they ate and drank different plants and waters, respectively, and thus did not migrate among regions. Results in italics were first published by Fricke et al. (2008).

Variable 1	Variable 2	<i>p</i> -value	Significant?
<i>JR hadro, enamel, oxygen</i>	<i>JR gar, ganoine, oxygen</i>	0.03	yes
<i>JR hadro, enamel, carbon</i>	<i>JR hadro, ganoine, carbon</i>	0.00	yes
<i>DP hadro, enamel, oxygen</i>	<i>DP gar, ganoine, oxygen</i>	0.00	yes
<i>DP hadro, enamel, carbon</i>	<i>DP hadro, ganoine, carbon</i>	0.11	no
<i>TM hadro, enamel, oxygen</i>	<i>TM gar, ganoine, oxygen</i>	0.00	yes
<i>TM hadro, enamel, carbon</i>	<i>TM hadro, ganoine, carbon</i>	0.02	yes
KA hadro, enamel, oxygen	KA gar, ganoine, oxygen	0.01	yes
KA hadro, enamel, carbon	KA hadro, ganoine, carbon	0.00	yes
FR hadro, enamel, oxygen	FR gar, ganoine, oxygen	0.01	yes
FR hadro, enamel, carbon	FR hadro, ganoine, carbon	0.01	yes
FR bivalve, carbon	FR gar, ganoine, carbon	0.00	yes
FR bivalve oxygen	FR gar, ganoine, oxygen	0.59	no

nations include (1) physiological differences among hadrosaurid species, and (2) limited movement of hadrosaurids between regions.

Diagenesis.—Post-depositional alteration of stable isotope ratios is intimately related to flow of fluids through sediments that either can undergo isotopic exchange with bioapatite or can facilitate the precipitation of authigenic carbonates between bioapatite crystals (e.g., Zazzo et al. 2004). Whether fluid flow affected a given set of sediments is determined not by the age of the sediments, but rather by their burial history and association with pathways for fluid flow (e.g., faults, veins). As a result there is no a priori reason to expect Cretaceous-aged fossils to be any more or less affected by diagenetic alteration than Quaternary-aged fossils.

Ideally an unambiguous test for the occurrence of isotopic alteration would exist, but it does not (Kohn and Cerling 2002). For this reason, the goal here is to demonstrate *not* that isotopic alteration is absent, but instead that diagenesis hasn't entirely obscured original paleobiological information reflected in stable isotope ratios of biogenic apatite. Fricke et al. (2008) and Fricke and Pearson (2008) outlined several methods for doing this, including the identification of primary aragonite and comparisons of isotopic data (1) between enamel and authigenic carbonate, (2) between enamel and dentine from the same fossil element, and (3) among invertebrate and vertebrate taxa. Fricke et al. (2008) presented evidence that diagenesis did not obscure original isotopic information in hadrosaurid tooth enamel and

TABLE 6. Statistical comparisons of isotopic data from hadrosaur enamel *among formations* (variable 1 and variable 2). See Table 4 for statistical tests used. When $p < 0.05$, populations are considered to be significantly different from each other. The occurrence of significant isotopic differences among hadrosaurids indicates that they ate and drank different plants and waters, respectively, and thus did not migrate among regions.

Variable 1	Variable 2	<i>p</i> -value	Significant?
JR hadro, enamel, carbon	FR hadro, enamel, carbon	0.00	yes
JR hadro, enamel, oxygen	FR hadro, enamel, oxygen	0.76	no
DP hadro, enamel, carbon	FR hadro, enamel, carbon	0.00	yes
DP hadro, enamel, oxygen	FR hadro, enamel, oxygen	0.00	yes
JR hadro, enamel, carbon	DP hadro, enamel, carbon	0.38	no
JR hadro, enamel, oxygen	DP hadro, enamel, oxygen	0.00	yes
KA hadro, enamel, carbon	FR hadro, enamel, carbon	0.00	yes
KA hadro, enamel, oxygen	FR hadro, enamel, oxygen	0.71	no
TM hadro, enamel, carbon	FR hadro, enamel, carbon	0.75	no
TM hadro, enamel, oxygen	FR hadro, enamel, oxygen	0.00	yes
TM hadro, enamel, carbon	DP hadro, enamel, carbon	0.00	yes
TM hadro, enamel, oxygen	DP hadro, enamel, oxygen	0.00	yes

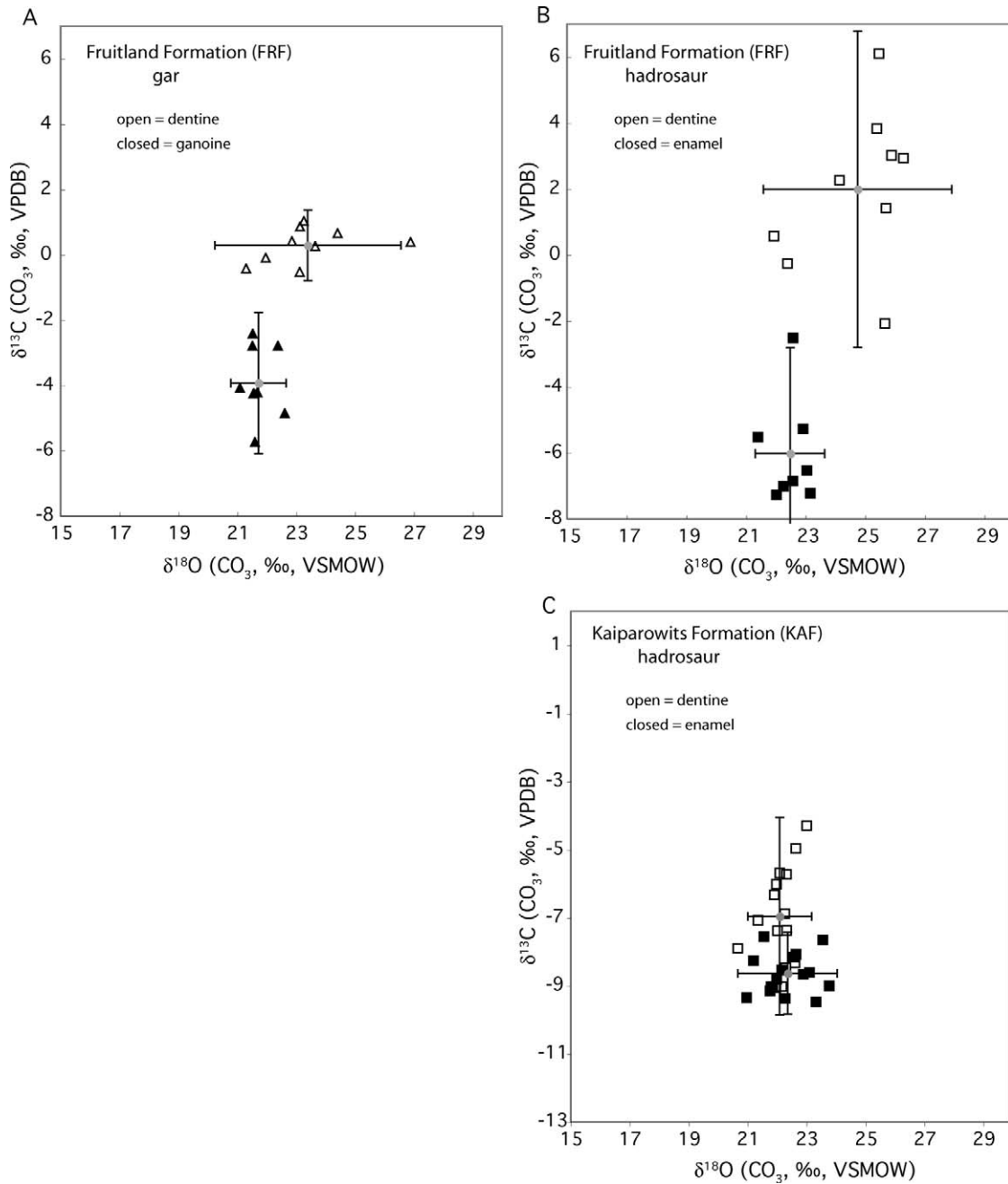


FIGURE 4. Comparisons of isotope data from hadrosaurid tooth enamel/gar scale ganoine and from dentine of the same tooth/scale (averages $\pm 2\sigma$ illustrated by cross). A, Gar scales from the FRF. B, Hadrosaurid teeth from the FRF. C, Hadrosaurid teeth from the KAF. In all cases, dentine is characterized by higher carbon 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.

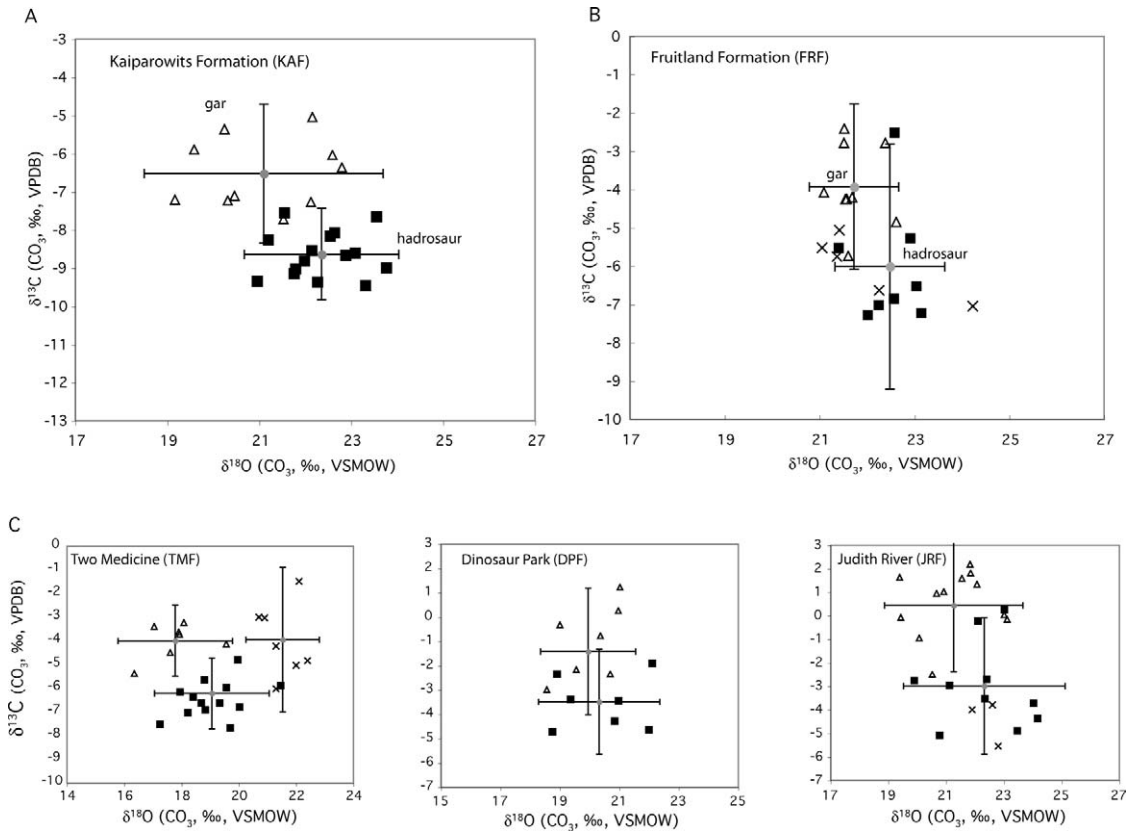


FIGURE 5. Isotopic comparison of enamel, ganoine, and aragonite from coexisting hadrosaurids (squares), gars (triangles), and bivalves (crosses), respectively (averages $\pm 2\sigma$ illustrated by cross). Samples from the KAF (A), the FRF (B), and the TMF, DPF, and JRF (C) (data from Fricke et al. 2008). All exhibit similar isotopic relations between taxa, with gar having higher carbon isotope ratios and lower oxygen isotope ratios. 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, and partial overprinting should result in taxonomic offsets that parallel the enamel-dentine trends of Figure 4. Thus, the occurrence of these taxonomic differences is evidence that complete isotopic resetting did not occur.

gar ganoine collected from the TMF, DPF, and JRF. Therefore, further discussion of diagenesis in this paper is focused on the newly sampled hadrosaurid material from the KAF and FRF.

The occurrence of aragonitic mollusc shells provides an indirect measure of diagenesis within a formation. After the death of the organism, biogenic aragonite readily recrystallizes to form calcite at moderate temperatures and pressures. Thus, the presence of this metastable mineral in terrestrial sediments of the Judith River, Two Medicine, and Fruitland Formations is a strong indicator that those systems have not undergone intensive diagenesis related to burial or fluid flow (Dettman and Lohmann 2000; Fricke et al. 2008). In the cases

of the Kaiparowits Formation, the absence of authigenic carbonates such as paleosol carbonate nodules and sparry calcite cement indicates that carbonate mobility in these sediments was limited.

A more direct measure of the impact of diagenesis in KAF and FRF fossils is the comparison of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in dentine and enamel/ganoine from the same skeletal elements (i.e., the same tooth or scale; Fig. 4). The rationale behind such a comparison of isotopic data is that dentine has smaller crystal sizes and a more porous structure than enamel (and the homologous ganoine), and as a result it is more susceptible to diagenetic alteration (Fricke 2007; Fricke et al. 2008; Fricke and Pearson 2008 and references therein). Thus, isotopic

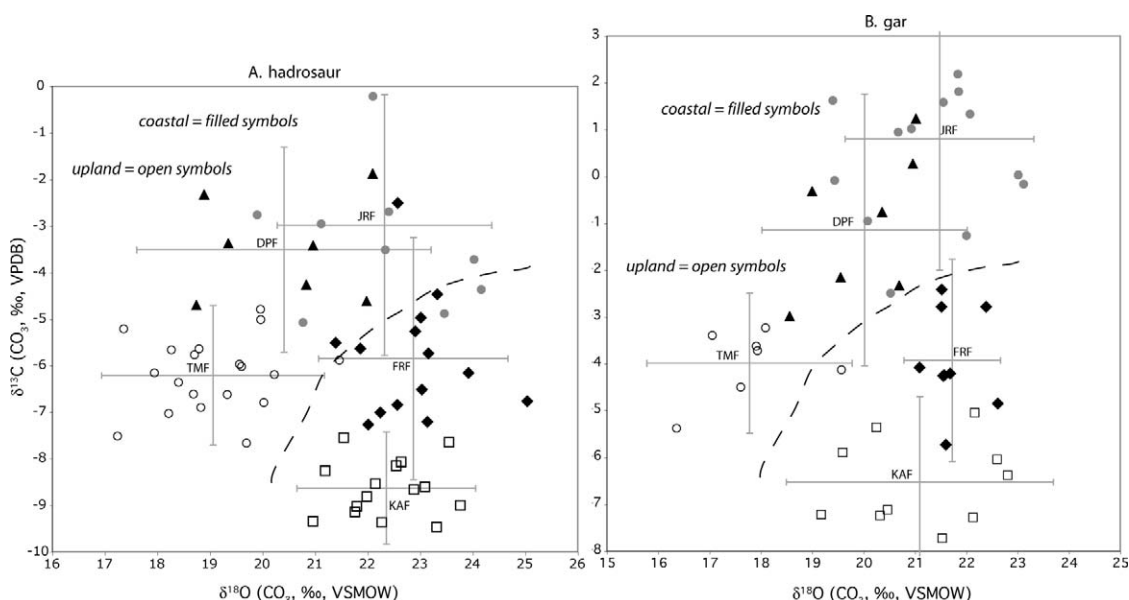


FIGURE 6. Comparison of isotope data from hadrosaurid tooth enamel (A) and gar scale ganoine (B) among all five formations (averages $\pm 2\sigma$ illustrated by cross). Dashed lines separate lower-latitude and higher-latitude east-west transects (see Fig. 3). Lack of significant isotopic overlap for hadrosaurid populations indicates that they did not undertake upland-coastal migrations, and that north-south migrations, if they did occur, were less than ~ 1000 km. Similar isotopic patterns for gar, which are assumed to be non-migratory, are consistent with these interpretations of hadrosaur behavior. Paleoenvironmental implications of these data have been discussed in more detail in the case of the TMF, DPF, and JRF (Fricke et al. 2008), and a more detailed paleoenvironmental discussion of data from KAF and FRF will be provided in a separate publication. Note that increasing $\delta^{13}\text{C}$ of plants with latitude is opposite the trend observed for the present day (Fig. 2), and this indicates that diagenesis by recent groundwaters cannot account for patterns in Cretaceous data. See Figure 5 for description of symbols.

differences between dentine and enamel can be used to address the differential preservation of the latter. In general, the dentine samples used in this study are characterized by higher isotope ratios and greater variability in measured ratios of both oxygen and carbon isotopes than those for hadrosaurid enamel and gar ganoine (Table 3, Fig. 4). Similar isotopic relations between enamel and dentine have been also observed for hadrosaurid remains of somewhat younger age in eastern Montana (Stanton-Thomas and Carlson 2004) and for hadrosaurids and gar from the TMF, DPF, and JRF (Table 2) (Fricke et al. 2008).

The greater variability and higher isotopic ratios of dentine relative to enamel suggest that dentine has been subject to a larger degree of isotopic exchange and/or mineral infilling than enamel, although this isotopic modification is not uniform in nature. In contrast, diagenetic processes were not pervasive enough to modify original ranges in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of enamel to the same degree. It is im-

portant to note that although dentine is more susceptible to diagenetic alteration, there is no reason to expect that all diagenetically altered samples will obtain the exact same isotope ratios, or that they will necessarily have isotope ratios that fall outside the range for enamel (e.g., Fig. 4C). It is possible that variable porosity and permeability of surrounding sediment variably inhibited the flow and amount of diagenetic fluids that interacted with different tooth fragments. Furthermore, the precipitation of secondary carbonate can itself gradually reduce porosity and permeability of skeletal materials (Trueman and Tuross 2002; Trueman et al. 2004), thus making it unlikely that all dentine will have the exact same diagenetic history and thus the exact same isotope ratio.

The strongest evidence against diagenetic overprinting comes from a comparison of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of enamel/ganoine among coexisting taxa (Fig. 5). Significant and consistent offsets are observed between hadrosaurids and

gar, and associated bivalves typically have isotope ratios that are different than one or both co-occurring vertebrates (Fig. 5). It is interesting to note that the direction of offsets between site-specific hadrosaurid-gar pairs are generally the same in all five sampled sites, regardless of absolute isotope ratio, with gar scales having lower $\delta^{18}\text{O}$ and higher $\delta^{13}\text{C}$ relative to hadrosaurs (Fig. 5). This consistent pattern suggests that the offsets reflect physiological and/or ecological differences among taxa, such as those observed for vertebrates occupying terrestrial C3 ecosystems of the past (MacFadden and Higgins 2004; Feranec and MacFadden 2006) and present (Bocherens 2003; Cerling et al. 2004).

A discussion of exact physiological/ecological meaning of these taxonomic offsets is beyond the scope of this paper, but it is not necessary to have an a priori understanding of them. The critical point is that isotopic offsets can be preserved only if isotopic alteration does not entirely obscure the original pattern of isotopic data. If, in contrast, isotopic alteration *was* extensive in any one of these formations, then enamel, ganoine, and aragonite should have much more similar isotopic ratios, because isotopic exchange with ground waters or secondary precipitation of apatite during diagenesis conditions would result in near-uniform isotope ratios for a single microfossil bonebed, regardless of taxonomic or ecologic affinity. Even partial, or differential, diagenesis between enamel and ganoine is unlikely, because the offsets observed between enamel/ganoine and dentine (*both* $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of dentine are typically higher relative to enamel/ganoine; Fig. 4 [see also Fricke et al. 2008]) are in the opposite direction than the taxonomic offsets (gar scales having *lower* $\delta^{18}\text{O}$ and higher $\delta^{13}\text{C}$ relative to hadrosaurs; Fig. 5).

In summation, none of the isotopic comparisons described above provide conclusive evidence that original paleobiological information is retained in enamel-ganoine isotope data. However, when isotopic offsets from all materials, from all taxa, and from all formations are considered together as a whole rather than as separate "tests," the most parsimonious interpretation of these data is that primary isotopic signals have been preserved,

and thus diagenetic overprinting by regional groundwaters does not fully explain the isotopic differences among hadrosaurids collected from each formation.

Physiological Differences among Hadrosaurid Taxa.—Another possible explanation for the differences in isotopic ratios of hadrosaurid tooth enamel among formations (Fig. 6A) is that hadrosaurid species in different regions varied greatly in physiology. Despite the relatively little overlap in fossil occurrence of hadrosaurid taxa among the study formations (Table 1) (Weishampel et al. 2004), if one hypothesizes that each taxon utilized ingested carbon and oxygen in a different manner, then different $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of enamel could result even if the different species ate and drank from similar sources.

It is not possible to provide direct evidence against this hypothesis, but there are several reasons why physiological differences are unlikely to explain all the isotopic variability observed. First, in large mammalian ungulates within an isotopically homogeneous ecosystem, $\delta^{18}\text{O}$ values are statistically indistinguishable (Hoppe et al. 2004; Hoppe 2006), and $\delta^{13}\text{C}$ values do not vary by more than ~2‰ (e.g., Cerling and Harris 1999; Passey et al. 2005), even for animals that are phylogenetically very different. These data suggest that physiological differences in oxygen and carbon utilization by large animals is phylogenetically conservative, and that physiology is unlikely to account for the range in average isotope ratios of ~2–6‰ observed in this study. A second, albeit more indirect, argument against a physiological cause of isotopic differences among taxa is the observation that $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of hadrosaurids vary in a regular manner with their position relative to the coast. In particular, hadrosaurids from lowland coastal areas have higher $\delta^{18}\text{O}$, and more consistently higher $\delta^{13}\text{C}$, than those from inland and upland localities (Fig. 6A). These isotopic patterns match those predicted to occur as a result of environmental differences between localities, as higher $\delta^{18}\text{O}$ and higher $\delta^{13}\text{C}$ are expected for surface waters and plants from coastal lowland environments along the inland seaway, whereas lower $\delta^{18}\text{O}$ and lower $\delta^{13}\text{C}$ are predicted for surface wa-

ters and plants from upland alluvial floodplain settings (Fricke et al. 2008). The alternative explanation, that these patterns instead reflect physiological differences among hadrosaurid species that move freely among regions, would require a high degree of serendipity.

Limited Geographic Migration by Hadrosaurids.—On the basis of the arguments presented above, we believe that the most likely explanation for isotopic differences observed among hadrosaurid remains collected in different areas is that, the geographic ranges of living hadrosaurs were limited to relatively small regions. Although these coastal-upland trends have been noted previously (Fricke et al. 2008), results from this study allow for latitudinal trends to be described as well. In particular, higher-latitude localities (TMF, DPF, JRF) have lower $\delta^{18}\text{O}$ and higher $\delta^{13}\text{C}$ than their more southern counterparts. A decrease in $\delta^{18}\text{O}$ with latitude reflects the rainout of air masses moving from tropical to polar regions (Dansgaard 1964; Rozanski et al. 1993; Gat 1996) and is not unexpected. An increase in $\delta^{13}\text{C}$ of plants with latitude (Fig. 6), however, is opposite the trend observed for the present day (Fig. 2). This difference reflects the absence of C4 plants during the Late Cretaceous, and a possible increase in the proportion of gymnosperms to angiosperms occupying the landscape at higher latitudes (which was the case for the early Cretaceous [Crane and Lidgard 1989]). Thus, each area represented a distinct isotopic domain (e.g., Fig. 1) that was in turn reflected in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of hadrosaurian tooth enamel. Slow rates of hadrosaur tooth mineralization should ensure that these isotopic domains reflect a multi-year isotopic history of food and water intake, rather than an isotopic “snapshot” of their most recent area of occupation.

Data from gar scale ganoine, which mirror the patterns observed for hadrosaurs (Fig. 6B), support the interpretation that variable environmental conditions from place to place were the main cause of observed patterns in hadrosaurid isotopic data. The diet and physiology of these fish were no doubt different from those of coexisting hadrosaurid species; thus the similarity in isotopic patterns between

these taxa argues for an external, or environmental, cause of isotopic differences. In addition, populations of freshwater fish like gar were probably endemic rather than migratory, and thus the similarity in isotopic patterns for hadrosaurs and gar (Fig. 6A,B) are consistent with the premise that hadrosaurid migration was limited in scope.

Behavioral Implications

Stable isotope data presented in this report suggest that populations of hadrosaurids were limited in their geographic distribution, and that migration (to the extent that mixing of isotopic domains would occur) was unlikely. Our findings based on isotope data can be considered along with fossil distribution data to address previous hypotheses regarding hadrosaurid behavior.

Nesting Localities and Coastal-Upland Migrations.—Hadrosaurid nesting sites (particularly those of *Maiasaura peeblesorum* and *Hypacrosaurus stebingeri*) are relatively common in the “upland coastal plain habitats” of the Two Medicine Formation (Horner and Makela 1979; Horner et al. 1984; Horner and Currie 1994), prompting hypotheses of preferred upland habitats for nesting and rearing of young and consequent seasonal migrations to and from such upland “rookeries” (Matthew 1915; Horner and Makela 1979; Horner 1984, 1989). The subsequent discovery of hadrosaur nesting sites in the Judith River Formation (Clouse and Horner 1993; Horner 1998, 1999) demonstrated that hadrosaurids also nested in the contemporaneous coastal-plain lowlands, but lent little insight into the debate surrounding potential migrations to and from preferred nesting regions.

The fossil localities studied here include two coastal-upland transects, one to the north (JRF, DPF, TMF) and one to the south (FRE, KAF). In neither case is there isotopic overlap between hadrosaurid samples collected from upland areas and coastal settings (Fig. 6A). The implications of these data are that hadrosaurs yielding teeth in any given area had not spent significant time feeding or ingesting water from “foreign” isotopic domains or environmental settings (upland versus lowland) (Fig. 7). If hadrosaurids had been migrating

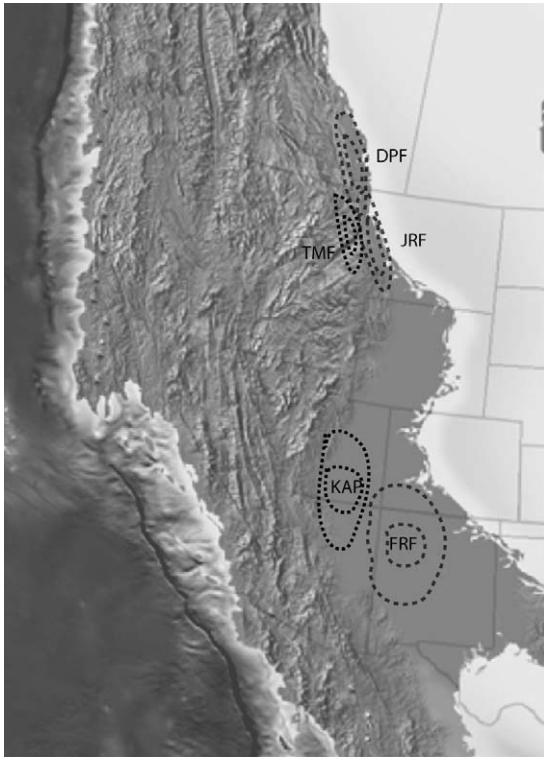


FIGURE 7. Limited isotopic overlap for data from hadrosaurid tooth enamel indicates that these animals were restricted in their distribution, particularly in movement between upland and coastal areas (upland areas are the western set of circles and coastal areas the eastern set of circles in each pair). It is difficult at this time, however, to provide exact limits on north-south movements, an uncertainty that is reflected by rings of different sizes surrounding each sampled location.

between upland “rookeries” and lowland habitats in relation to some reproductive strategy, some degree of isotopic overlap or mixing would be expected. Moreover, if long-distance migration from the alluvial uplands to the coastal plain lowlands had been the norm, the fossil remains of migratory taxa would be expected to occur in rocks throughout the study area. However, faunal lists compiled for the targeted interval (see Table 1) indicate that exceedingly few hadrosaurian taxa are shared among localities.

Assuming these isotope-based inferences related to hadrosaur movement are correct, then hadrosaurid nesting must have been common in both coastal and upland settings. The relative scarcity of lowland nesting locales thus likely reflects taphonomic bias (Car-

penter 1982), as opposed to an ecological strategy.

North-South Migrations.—It has also been suggested that hadrosaurids may have moved north-south, parallel to the shoreline of the Western Interior Seaway (Hotton 1980). In this way, they would have been able to remain in their generally preferred habitat zones such as coastal swamp or upland floodplain (Fig. 2). The geographic distribution of fossil localities studied here includes two north-south transects, one to the west (TMF-KAF) and one to the east (DPF, JRF, FRF) thus allowing for an initial test of this hypothesis.

In the case of the inland and upland TMF and KAF, the lack of isotopic overlap again indicates that hadrosaurids shedding teeth in these ~1400 km distant areas did not eat food or ingest water from “foreign” isotopic domains. Although these results provide constraints on long-distance north-south hadrosaurid movement between present-day Montana and Utah, the present geographic sampling makes it impossible to rule out the possibility that upland hadrosaurids migrated over shorter distances (Fig. 7). Therefore, future research efforts should focus on sampling the spatial gaps so that patterns of movement can be better constrained.

The spatial resolution of sampled localities is slightly better for the more coastal DPF, JRF, and FRF, particularly in the north portion of the study interval. The lack of significant isotopic overlap between the JRF and FRF again suggests that migration of hadrosaurid taxa did not occur over distances of several hundreds of kilometers. More intriguing are the isotopic relations between the DPF and JRF. A significant difference in average $\delta^{18}\text{O}$ values does exist between these two units. In contrast, there is a great deal of isotopic overlap in $\delta^{13}\text{C}$ between formations (Fig. 6A). The former suggests that two distinct populations are being sampled, whereas the latter is consistent with two possible interpretations. One is that some hadrosaurid individuals shared the same dietary and water resources, and thus must have traveled at least part of the ~300 km distance between the two areas. Alternatively, there may have been two geographically distinct populations of animals that con-

sumed plants and waters that were isotopically similar. At this time it is not possible to determine which of these two scenarios is more likely, and they need not be mutually exclusive.

Finally, with regard to polar dinosaurs and the likelihood of long-distance migration, we are not able to address the question directly with the isotopic data at hand. This is an unfortunate limitation of the current study, because the discovery of polar dinosaurs (Rich et al. 1988; Nelms 1989; Hammer and Hickerson 1993, 1994; Molnar and Wiffen 1994; Slaughter et al. 1994; Gangloff 1995; Case et al. 2000; Fiorillo and Gangloff 2003; Gangloff and Fiorillo 2003; Fiorillo and Parrish 2004; Gangloff et al. 2005), and the inherent implications of their high-latitude ecology (e.g., 24-hour darkness in winter, strong seasonal fluctuations in primary productivity), essentially ignited the current debate on dinosaur migration. In a recent comprehensive review of the topic, Bell and Snively (2008) explored a variety of data sets in an effort to resolve whether dinosaurs migrated long distances (up to 30° latitude) in response to the ecological hardships of high-latitude existence, or whether they remained more localized and overwintered. These authors concluded that subsistence overwintering, specifically in the case of the presumably insular Late Cretaceous dinosaur fauna of New Zealand (Molnar and Wiffen 1994), was the only behavioral strategy presently supported by “conclusive evidence.” Future comparative studies such as ours that include isotopic data sets derived from polar localities in Alaska, Antarctica, New Zealand, and elsewhere promise to yield additional key insights into the question of dinosaur migration and ecology.

Summary

Stable isotope data derived from hadrosaurid tooth enamel recovered from several contemporaneous localities in the Western Interior foreland basin allow for novel reconstructions that relate to geographic range and migratory behavior. Specific insights provided by this isotope-based study include a test of the hypothesis that hadrosaurids of the Western Interior Basin did not undertake long-

range east-west migrations in order to utilize preferred nesting grounds. Furthermore, there is no clear indication that hadrosaurids migrated long distances in north-south belts paralleling the Western Interior Seaway in order to track resources. These paleoecological inferences are arguably reasonable given the isotopic data recovered, and are certainly consistent with data relating to the geographic distribution of hadrosaurid remains themselves (Weishampel et al. 2004). Nevertheless, we recognize that more work is needed. In particular, spatial gaps in our sampling, coupled with limits in temporal resolution, prevent a more complete understanding of distributional patterns at this time. Future studies of hadrosaurid remains from Alaska, Texas, and Mexico will expand our geographic coverage, and investigations of specific hadrosaur species can increase our taxonomic resolution. The potential also exists to expand this type of isotopic study to include other dinosaurs, including ceratopsians and theropods. Finally, observation that such correspondence between isotopic and fossil distribution exists encourages the use of similar stable isotope approaches in places and time periods where the fossil record may not offer significant skeletal specimens.

Acknowledgments

This work could not be done without the help of D. Brinkman, J. Eaton, D. Eberth, M. Getty, J. Mitchell, S. D. Sampson, and T. Williamson, who provided access to fossils and valuable information regarding their geologic and paleontological context, and we thank them all. Comments that helped improve the paper were given by D. Evans and W. Straight. Financial support was provided by National Science Foundation EAR-0319024, National Science Foundation EAR-0319041, American Chemical Society–Petroleum Research Fund 38141-GB8, Colorado College, and Macalester College.

Literature Cited

- Badgley, C. 1986. Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan. *Paleobiology* 12:119–142.
- Barrera, E., and S. M. Savin. 1999. Evolution of late Campanian–Maastrichtian marine climates and oceans. Pp. 245–282 *in* E. Barrera and C. C. Johnson, eds. *Evolution of the Cretaceous*

- ocean-climate system. *Geological Society of America Special Paper* 332:242–282.
- Bell, P. R., and E. Snively. 2008. Polar dinosaurs on parade: a review of dinosaur migration. *Alcheringa* 32:271–284.
- Bocherens, H. 2003. Isotopic biogeochemistry and the paleoecology of the mammoth steppe fauna. *Deinsea* 9:57–76.
- Bryant, J. D., and P. N. Froelich. 1995. A model of oxygen isotope fractionation in body water of large mammals. *Geochimica et Cosmochimica Acta* 59:4523–4537.
- Brouwers, E. M., W. A. Clemens, R. A. Spicer, T. A. Ager, D. L. Carter, and W. V. Sliter. 1987. Dinosaurs on the North Slope of Alaska: high latitude, latest Cretaceous environments. *Science* 237:1608–1610.
- Carpenter, K. 1982. Baby dinosaurs from the Late Cretaceous Lance and Hell Creek Formations and a description of a new species of theropod. *University of Wyoming Contributions to Geology* 20(2):23–134.
- Case, J. A., J. E. Martin, D. S. Chaney, M. Reguero, S. A. Marenssi, S. M. Santillana, and M. O. Woodburne. 2000. The first duck-billed dinosaur (family Hadrosauridae) from Antarctica. *Journal of Vertebrate Palaeontology* 20:612–614.
- Cerling, T. E., and J. M. Harris. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120:347–363.
- Cerling, T. E., J. A. Hart, and T. B. Hart. 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* 138:5–12.
- Clemens, W. A., and C. W. Allison. 1985. Late Cretaceous terrestrial vertebrate fauna, North Slope, Alaska. *Geological Society of America Abstracts with Programs* 17(7):548.
- Clemens, W. A., and L. G. Nelms. 1993. Paleocological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high latitudes. *Geology* 21:503–506.
- Clementz, M. T., and P. L. Koch. 2001. Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. *Oecologia* 129:461–472.
- Clouse, V., and J. R. Horner. 1993. Eggs and embryos from the Judith River Formation of Montana. *Journal of Vertebrate Paleontology* 13(Suppl. 3):31A.
- Crane, P. R., and S. Lidgard. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science* 246:675–678.
- Currie, P. J. 1989. Dinosaur footprints of western Canada. Pp. 293–307 in D. D. Gillette and M. G. Lockley, eds. *Dinosaur tracks and traces*. Cambridge University Press, Cambridge.
- Dansgaard, W. 1964. Stable isotopes in precipitation. *Tellus* 16:436–468.
- Davies, K. L. 1987. Duck-bill dinosaurs (Hadrosauridae, Ornithischia) from the North Slope of Alaska. *Journal of Paleontology* 61:198–200.
- DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42:495–506.
- Dettman, D. L., and K. Lohmann. 2000. Oxygen isotope evidence for high-altitude snow in the laramide Rocky Mountains of North America during the Late Cretaceous and Paleogene. *Geology* 28:243–246.
- Eberth, D. A. 2005. The geology. Pp. 54–82 in P. J. Currie and E. B. Koppelhus, eds. *Dinosaur Provincial Park*. Indiana University Press, Bloomington.
- Eberth, D. A., and A. L. Deino. 1992. A geochronology of the non-marine Judith River Formation of southern Alberta. SEPM 1992 theme meeting, Mesozoic of the Western Interior, Fort Collins, Abstracts with Programs, pp. 24–25.
- Eberth, D. A., and A. P. Hamblin. 1993. Tectonic, stratigraphic, and sedimentological significance of a regional discontinuity in the Upper Judith River Group (Belly River wedge) of southern Alberta, Saskatchewan, and northern Montana. *Canadian Journal of Earth Sciences* 30:174–200.
- Eberth, D. A., and A. L. Deino. 2005. New ⁴⁰Ar/³⁹Ar ages from three bentonites in the Bearpaw, Horseshoe Canyon, and Scollard formations (Upper Cretaceous–Paleocene) of southern Alberta, Canada. Pp. 23–24. in D. R. Braman, F. Therrien, E. B. Koppelhus, and W. Taylor, eds. *Dinosaur Park Symposium: Short papers, abstracts, and program*. Royal Tyrrell Museum of Paleontology, Drumheller, Alberta.
- Eberth, D. A., R. R. Rogers, and A. R. Fiorillo. 2007. A practical approach to the study of bonebeds. Pp. 265–332 in D. A. Eberth, R. R. Rogers, and A. R. Fiorillo, eds. *Bonebeds*. University of Chicago Press, Chicago.
- Epstein, S., and T. Mayeda. 1953. Variations in the 18-O content of waters from natural sources. *Geochimica et Cosmochimica Acta* 4:213–224.
- Erickson, G. M. 1996. Incremental lines of von Ebner in dinosaurs and the assessment of tooth replacement rates using growth line counts. *Proceedings of the National Academy of Sciences USA* 93:14623–14627.
- Evans, D. C., and R. R. Reisz. 2007. Anatomy and relationships of *Lambeosaurus magnicristatus*, a crested hadrosaurid dinosaur (Ornithischia) from the Dinosaur Park Formation, Alberta. *Journal of Vertebrate Paleontology* 27:373–393.
- Farquhar, G. D., Ehleringer, J. R., and Hubick, K. T. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40:503–37.
- Feranec, R. S., and B. J. MacFadden. 2006. Isotopic discrimination of resource partitioning among ungulates in C3-dominated communities from the Miocene of Florida and California. *Paleobiology* 32:191–205.
- Fiorillo, A. R., and R. A. Gangloff. 2001. The caribou migration model for Arctic hadrosaurs (Ornithischia: Dinosauria): a reassessment. *Historical Biology* 15:323–334.
- . 2003. Preliminary notes on the taphonomic and ecologic setting of a Pachyrhinosaurus bonebed in northern Alaska. *Journal of Vertebrate Paleontology* 23:50A.
- Fiorillo, A. R., and J. T. Parish. 2004. The first record of a Cretaceous dinosaur from southwestern Alaska. *Cretaceous Research* 25:453–458.
- Foreman, B. Z., R. R. Rogers, A. L. Deino, K. R. Wirth, and J. T. Thole. 2008. Geochemical characterization of bentonite beds in the Two Medicine Formation (Campanian, Montana), including a new ⁴⁰Ar/³⁹Ar age. *Cretaceous Research* 29:373–385.
- Fricke, H. C. 2007. Stable isotope geochemistry of bonebed fossils: reconstructing paleoenvironments, paleoecology, and paleobiology. Pp. 437–490 in R. R. Rogers, D. A. Eberth, and A. R. Fiorillo, eds. *Bonebeds: genesis, analysis, and paleobiological significance*. University of Chicago Press, Chicago.
- Fricke, H. C., and J. R. O’Neil. 1996. Inter- and intra-tooth variations in the oxygen isotope composition of mammalian tooth enamel: some implications for paleoclimatological and paleobiological research. *Palaeogeography, Palaeoclimatology, Palaeoecology* 126:91–99.
- Fricke, H. C., and D. A. Pearson. 2008. Stable isotope evidence for changes in dietary niche partitioning among hadrosaurian and ceratopsian dinosaurs of the Hell Creek Formation, North Dakota. *Paleobiology* 34:534–552.
- Fricke, H. C., W. C. Clyde, J. R. O’Neil, and P. D. Gingerich. 1998. Intra-tooth variation in $\delta^{18}\text{O}$ of mammalian tooth enamel as a record of seasonal changes in continental climate variables. *Geochimica et Cosmochimica Acta* 62:1839–1851.
- Fricke, H. C., R. R. Rogers, R. Backlund, C. N. Dwyer, and S. Echt. 2008. Preservation of primary stable isotope signals in dinosaur remains, and environmental gradients of the Late Cretaceous of Montana and Alberta. *Palaeogeography, Palaeoclimatology, Palaeoecology* 266:13–27.

- Gangloff, R. A. 1995. *Edmontonia* sp., the first record of an ankylosaur from Alaska. *Journal of Vertebrate Palaeontology* 15: 195–200.
- Gangloff, R. A., and A. R. Fiorillo. 2003. The record of Arctic dinosaurs from northern Alaska, paleogeographic and paleoecologic implications. *Journal of Vertebrate Palaeontology* 23: 53A.
- Gangloff, R. A., A. R. Fiorillo, and D. W. Norton. 2005. The first pachycephalosaurine (Dinosauria) from the Arctic of Alaska and its paleogeographic implications. *Journal of Paleontology* 79:997–1001.
- Gannes, L. Z., C. M. de Rio, and P. Koch. 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. *Comprehensive Biochemical Physiology A* 119A:725–737.
- Gat, J. R. 1996. Oxygen and hydrogen isotopes in the hydrologic cycle. *Annual Review of Earth and Planetary Sciences* 24:225–262.
- Gates, T. A., and D. C. Evans. 2005. Biogeography of Campanian hadrosaurid dinosaurs from western North America. Pp. 33–39 in D. R. Braman, F. Therrien, E. B. Koppelhus, and W. Taylor, eds. *Dinosaur Park Symposium short papers, abstracts, and programs*. Royal Tyrrell Museum of Paleontology, Drumheller, Alberta.
- Hammer, W. R., and W. J. Hickerson. 1993. A new Jurassic dinosaur fauna from Antarctica. *Journal of Vertebrate Palaeontology* 13:40A.
- . 1994. A crested theropod dinosaur from Antarctica. *Science* 264:828–830.
- Hedges, R. E. M. 2003. On bone collagen: apatite-carbonate isotopic relationships. *International Journal of Osteoarchaeology* 13:66–79.
- Hoppe, K. A. 2004. Late Pleistocene mammoth herd structure migration patterns and Clovis hunting strategies inferred from isotopic analyses of multiple death assemblages. *Paleobiology* 30:129–145.
- . 2006. Correlation between the oxygen isotope ratio of North American bison teeth and local waters: implication for paleoclimatic reconstructions. *Earth and Planetary Science Letters* 244:408–417.
- Hoppe, K. A., R. G. Amundson, M. Vavra, M. P. McClaran, and D. L. Anderson. 2004. Isotopic analysis of tooth enamel carbonate from modern North American feral horses: implications for paleoenvironmental reconstructions. *Palaeogeography, Palaeoclimatology, Paleoecology* 203:299–311.
- Hoppe, K. A., A. Paytan, and C. P. Chamberlain. 2006. Reconstructing grassland vegetation and paleotemperatures using carbon isotope ratios of bison tooth enamel. *Geology* 34:649–652.
- Horner, J. R. 1984. Three ecologically distinct vertebrate faunal communities from the Late Cretaceous Two Medicine Formation of Montana, with discussion of evolutionary pressures induced by interior seaway fluctuations. *Field Conference Guidebook*, pp. 299–304. Montana Geological Society, Billings.
- . 1989. The Mesozoic terrestrial ecosystems of Montana. *Field Conference Guidebook*, pp. 153–162. Montana Geological Society, Billings.
- . 1992. Cranial morphology of *Prosaurolophus* (Ornithischia: Hadrosauridae) with descriptions of two new hadrosaurid species and an evaluation of hadrosaurid phylogenetic relationships. *Museum of the Rockies Occasional Paper* 2:1–119.
- . 1998. An undisturbed clutch of hadrosaur eggs from the Judith River Formation of Montana. Pp. 22–25 in A. Golpim de Carvalho, M. Cachão, A. Andrade, C. da Silva, and V. dos Santos, eds. *Proceedings of the 1st International Meeting on Dinosaur Paleobiology* (May 26–29, 1998). Museu Nacional de Historia Natural, Universidade de Lisboa, Lisbon.
- . 1999. Egg clutches and embryos from two hadrosaurian dinosaurs. *Journal of Vertebrate Paleontology* 19:607–611.
- Horner, J. R., and P. J. Currie. 1994. Embryonic and neonatal morphology and ontogeny of a new species of *Hypacrosaurus* (Ornithischia, Lambeosauridae) from Montana and Alberta. Pp. 312–336 in K. Carpenter, K. F. Hirsch, and J. R. Horner, eds. *Dinosaur eggs and babies*. Cambridge University Press, Cambridge.
- Horner, J. R., and R. Makela. 1979. Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* 282: 296–298.
- Horner, J. R., J. G. Schmitt, F. Jackson, and R. Hanna. 2001. Bones and rocks of the Upper Cretaceous Two Medicine-Judith River Clastic Wedge Complex, Montana. In C. L. Hill, ed. *Field trip guidebook, Society of Vertebrate Paleontology 61st Annual Meeting: Mesozoic and Cenozoic Paleontology in the Western Plains and Rocky Mountains*. Museum of the Rockies Occasional Paper 3:3–14. Bozeman, Mont.
- Horner, J. R., D. B. Weishampel, and C. A. Forster. 2004. Hadrosauridae. Pp. 438–463 in D. B. Weishampel, P. Dodson and H. Osmolska, eds. *The Dinosauria*. University of California Press, Berkeley.
- Hotton, N., III. 1980. An alternative to dinosaur endothermy: the happy wanderers. Pp. 311–350 in R. D. K. Thomas and E. C. Olson, eds. *A cold-blooded look at warm-blooded dinosaurs*. Westview Press, Boulder, Colo.
- Jim, S., S. Ambrose, and R. Evershed. 2004. Stable carbon isotopic evidence for differences in the dietary origin of bone cholesterol, collagen and apatite: implications for their use in palaeodietary reconstruction. *Geochimica et Cosmochimica Acta* 68:61–72.
- Koch, P. L. 1998. Isotopic reconstruction of past continental environments. *Annual Review of Earth and Planetary Sciences* 26:573–613.
- Koch, P. L., Fogel, M., and Tuross, N. 1994. Tracing the diet of fossil animals using stable isotopes. Pp. 63–94 in K. Klajtha and R. H. Michener, eds. *Stable isotopes in ecology and environmental science*. Blackwell Scientific, Oxford.
- Koch, P. L., N. Tuross, and M. L. Fogel. 1997. The effects of sample treatment and diagnosis on the isotopic integrity of carbonate in biogenic hydroxyapatite. *Journal of Archaeological Sciences* 24:417–429.
- Kohn, M. J. 1996. Predicting animal $\delta^{18}\text{O}$: accounting for diet and physiological adaptation. *Geochimica et Cosmochimica Acta* 60:4811–4829.
- . 2006. REE and U zoning in fossil teeth. *Geological Society of America Abstracts with Programs* 38:46.
- Kohn, M. J., M. J. Schoeninger, and J. W. Valley. 1998. Variability in herbivore tooth oxygen isotope compositions: reflections of seasonality or developmental physiology? *Chemical Geology* 152:92–112.
- Kohn, M. J., and T. E. Cerling. 2002. Stable isotope compositions of biological apatite. *Reviews in Mineralogy and Geochemistry* 48:455–488.
- Lehman, T. M. 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America. *Palaeogeography, Palaeoclimatology, Paleoecology* 60:189–217.
- . 1997. Late Campanian dinosaur biogeography in the western interior of North America. Pp. 223–240 in D. L. Wolberg, E. Stump, and G. D. Rosenberg, eds. *Proceedings of the DinoFest International symposium*, Arizona State University. Academy of Natural Sciences, Philadelphia.
- . 2001. Late Cretaceous dinosaur provinciality. Pp. 310–328 in D. Tanke and K. Carpenter, eds. *Mesozoic vertebrate life*. Indiana University Press, Bloomington.

- Longinelli, A. 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? *Geochimica et Cosmochimica Acta* 48:385–390.
- Lucas, S. G., A. P. Hunt, and R. M. Sullivan. 2006. Stratigraphy and age of the Upper Cretaceous Fruitland Formation, west-central San Juan Basin, New Mexico. *In* S. G. Lucas and R. M. Sullivan, eds. Late Cretaceous vertebrates from the Western Interior. New Mexico Museum of Natural History and Science Bulletin 35:1–6.
- Luz, B., and Y. Kolodny. 1985. Oxygen isotope variations in phosphates of biogenic apatites. IV. Mammal teeth and bones. *Earth Planetary Science Letters* 75:29–36.
- MacFadden, B. J., and P. Higgins. 2004. Ancient ecology of 15-million-year-old browsing mammals within C3 plant communities from Panama. *Oecologia* 140:169–182.
- Matthew, W. D. 1915. Climate and evolution. *Annals of the New York Academy of Science* 24:171–318.
- Molnar, R. E., and J. Wiffen. 1994. A Late Cretaceous polar dinosaur fauna from New Zealand. *Cretaceous Research* 15: 689–706.
- Nelms, L. G. 1989. Late Cretaceous dinosaurs from the North Slope of Alaska. *Journal of Vertebrate Palaeontology* 9(Suppl. to No. 3):34A.
- O'Leary, M. H. 1988. Carbon isotopes in photosynthesis. *Bio-science* 38:328–336.
- O'Leary, M. H., S. Mahavan, and P. Paneth. 1992. Physical and chemical basis of carbon isotope fractionation in plants. *Plant, Cell and Environment* 15:1099–1104.
- Ogg, J. G., F. P. Agterberg, and F. M. Gradstein. 2004. *The Cretaceous Period*. Cambridge University Press, Cambridge.
- Parrish, J. M., J. T. Parrish, J. H. Hutchison, and R. A. Spicer. 1987. Late Cretaceous vertebrate fossils from the North Slope of Alaska and implications for dinosaur ecology. *Palaios* 2: 377–389.
- Passey, B. H., T. F. Robinson, L. K. Ayliffe, and T. E. Cerling, M. Sponheimer, M. D. Dearing, B. L. Roeder, and J. R. Ehleringer. 2005. Carbon isotope fractionation between diet, breath CO₂, and bioapatite in different mammals. *Journal of Archaeological Sciences* 32:1459–1470.
- Rich, P. V., T. H. Rich, B. E. Wagstaff, J. McEwan Mason, C. B. Douthitt, R. T. Gregory, and E. A. Felton. 1988. Evidence for low temperatures and biologic diversity in Cretaceous high-latitudes of Australia. *Science* 242:1403–1406.
- Roberts, E. M., A. L. Deino, and M. A. Chan. 2005. ⁴⁰Ar/³⁹Ar age of the Kaiparowits Formation, southern Utah, and correlation of contemporaneous Campanian strata and vertebrate faunas along the margin of the Western Interior Basin. *Cretaceous Research* 26:307–318.
- Rogers, R. R. 1990. Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of Montana: evidence for drought-related mortality. *Palaios* 5:394–413.
- . 1994. Nature and origin of through-going discontinuities in nonmarine foreland basin strata, Upper Cretaceous, Montana: implications for sequence analysis. *Geology* 22:1119–1122.
- . 1998. Sequence analysis of the Upper Cretaceous Two Medicine and Judith River formations, Montana: nonmarine response to the Claggett and Bearpaw marine cycles. *Journal of Sedimentary Research* 68:615–631.
- Rogers, R. R., and S. M. Kidwell. 2007. A conceptual framework for the genesis and analysis of vertebrate skeletal concentrations. Pp. 1–64 *in* R. R. Rogers, D. A. Eberth, and A. R. Fiorillo, eds. *Bonebeds*. University of Chicago Press, Chicago.
- Rogers, R. R., C. C. Swisher, and J. R. Horner. 1993. ⁴⁰Ar/³⁹Ar age and correlation of the non-marine Two Medicine Formation (Upper Cretaceous), northwestern Montana: Canadian *Journal of Earth Sciences* 30:1066–1075.
- Rozanski, K., L. Araguás-Araguás, and R. Gonfiantini. 1993. Isotopic patterns in modern global precipitation. Pp. 1–36 *in* P. K. Swart, K. C. Lohmann, J. McKenzie, and S. Savin, eds. *Climate change in the continental isotopic records*. American Geophysical Union, Washington, D.C.
- Ryan, M., and D. C. Evans. 2005. Ornithischian dinosaurs. Pp. 312–348 *in* P. J. Currie and E. B. Koppelhus, eds. *Dinosaur Provincial Park: a spectacular ancient ecosystem revealed*. Indiana University Press, Bloomington.
- Sharp, Z. D., and T. E. Cerling. 1998. Fossil isotope records of seasonal climate and ecology: straight from the horse's mouth. *Geology* 26:219–222.
- Slaughter, R. W., W. J. Hickerson, and W. R. Hammer. 1994. Analysis of Antarctic theropod teeth based on serration densities and patterns. *Geological Society of America Abstracts with Programs* 26:61.
- Stanton-Thomas, K., and S. J. Carlson. 2004. Microscale δ¹⁸O and δ¹³C isotopic analysis of an ontogenetic series of the hadrosaurid dinosaur *Edmontosaurus*: implications for physiology and ecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 206:257–287.
- Straight, W. H., R. E. Barrick, and D. A. Eberth. 2004. Reflections of surface water, seasonality and climate in stable oxygen isotopes from tyrannosaurid tooth enamel. *Palaeogeography, Palaeoclimatology, Paleocology* 206:239–256.
- Sullivan, R. M., and S. G. Lucas. 2006. The Kirtlandian land-vertebrate "age"-faunal comparison, temporal position and biostratigraphic correlation in the nonmarine Upper Cretaceous of western North America. *In* S. G. Lucas and R. M. Sullivan, eds. *Late Cretaceous vertebrates from the Western Interior*. New Mexico Museum of Natural History and Science Bulletin 35:7–30.
- Sullivan, R. M., and T. E. Williamson. 1999. A new skull of *Parasaurolophus* (Dinosauria: Hadrosauridae) from the Fruitland Formation of New Mexico and a revision of the genus. *New Mexico Museum of Natural History and Science Bulletin* 15: 1–52.
- Trueman, C. N., and N. Tuross. 2002. Trace elements in recent and fossil bone apatite. *Reviews in Mineralogy and Geochemistry* 48:489–521.
- Trueman, C. N., A. K. Behrensmeier, N. Tuross, and S. Weiner. 2004. Mineralogical and compositional changes in bones exposed on soil surfaces in Amboseli National Park, Kenya: diagenetic mechanisms and the role of sediment pore fluids. *Journal of Archaeological Science* 31:721–739.
- Weishampel, D. B., P. M. Barrett, R. A. Coria, J. Le Loeuff, X. Xing, Z. Xijin, A. Sahni, E. M. P. Goman, and C. R. Noto. 2004. Dinosaur distribution. Pp. 517–606 *in* D. B. Weishampel, P. Dodson, and H. Osmolska, eds. *The Dinosauria*. University of California Press, Berkeley.
- Williamson, T. E. 2000. Review of Hadrosauridae (Dinosauria, Ornithischia) from the San Juan Basin, New Mexico. Pp. 191–213 *in* S. G. Lucas and A. B. Heckert, eds. *Dinosaurs of New Mexico*. New Mexico Museum of Natural History and Science, Albuquerque.