Stable isotope evidence for changes in dietary niche partitioning among hadrosaurian and ceratopsian dinosaurs of the Hell Creek Formation, North Dakota

Henry C. Fricke and Dean A. Pearson

Abstract.—Questions related to dinosaur behavior can be difficult to answer conclusively by using morphological studies alone. As a complement to these approaches, carbon and oxygen isotope ratios of tooth enamel can provide insight into habitat and dietary preferences of herbivorous dinosaurs. This approach is based on the isotopic variability in plant material and in surface waters of the past, which is in turn reflected by carbon and oxygen isotope ratios of animals that ingested the organic matter or drank the water. Thus, it has the potential to identify and characterize dietary and habitat preferences for coexisting taxa.

In this study, stable isotope ratios from coexisting hadrosaurian and ceratopsian dinosaurs of the Hell Creek Formation of North Dakota are compared for four different stratigraphic levels. Isotopic offsets between tooth enamel and tooth dentine, as well as taxonomic differences in means and in patterns of isotopic data among taxa, indicate that primary paleoecological information is preserved. The existence of taxonomic offsets also provides the first direct evidence for dietary niche partitioning among these herbivorous dinosaur taxa. Of particular interest is the observation that the nature of this partitioning changes over time: for some localities ceratopsian dinosaurs have higher carbon and oxygen isotope ratios than hadrosaurs, indicating a preference for plants living in open settings near the coast, whereas for other localities isotope ratios are lower, indicating a preference for plants in the understory of forests. In most cases the isotope ratios among hadrosaurs are similar and are interpreted to represent a dietary preference for plants of the forest canopy. The inferred differences in ceratopsian behavior are suggested to represent a change in vegetation cover and hence habitat availability in response to sea level change or to the position of river distributaries. Given our current lack of taxonomic resolution, it is not possible to determine if dietary and habitat preferences inferred from stable isotope data are associated with single, or multiple, species of hadrosaurian/ceratopsian dinosaurs.

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Introduction

The Hell Creek Formation (HCF) is a fossil-rich package of terrestrial sedimentary rocks of latest Cretaceous age that is exposed throughout Montana, North Dakota, and South Dakota. Detailed studies in southwestern North Dakota indicate that a variety of sedimentary rock types are found throughout the HCF in this area, including poorly cemented channel and crevasse-splay sandstones, rooted siltstones, gray to brown mudstones, and some carbonaceous-rich shales, all of which are thought to represent meandering and laterally accreting fluvial channel systems and associated floodplains (Fastovsky 1987; Murphy et al. 2002). Oxygen isotope data from bivalves indicate that some of these larg-er 'trunk' rivers drained distant high-elevation areas, whereas smaller tributaries had more local sources of recharge (Dettman and Lohmann 2000). Invertebrate assemblages from the HCF reflect variable salinities that are consistent with these rivers being sometimes brackish and thus adjacent to an open marine interior seaway (Hartman and Kirtland 2002; Murphy et al. 2002), an interpretation that is supported by the occasional occurrence of marine-tolerant animals such as sharks, rays, and sawfish, as well as hesperornithiform birds in channel deposits (Murphy et al. 2002; Pearson et al. 2002).

This near-coastal setting offered a variety of microhabitats for plants to occupy, and a diverse megaflora dominated by angiosperms has been described for this area (Johnson

2002). Because most of these plants do not have extant relatives, and because some degree of taphonomic mixing of leaves from different habitats likely occurred (Johnson 2002), the exact nature of these Late Cretaceous plant communities remains somewhat obscure. Nevertheless, most of the preserved Hell Creek vegetation indicates that channel and floodplain environments were dominated by woodland forests made up of small to medium-sized trees, and that small herbaceous and shrubby plants occupied point bars of large river systems (Johnson 2002). In addition to such spatial differences in plant communities, there is evidence that the floral composition of forests changed over time, most likely in response to changes in climatic conditions (Johnson 2002). Mean annual temperatures in particular are estimated to have varied from 8° to 18°C in this area during Hell Creek time (Wilf et al. 2003).

In turn, plants of the HCF supported a variety of large herbivorous dinosaurs, with ceratopsians and hadrosaurids being among the best represented in southwestern North Dakota (Pearson et al. 2002). For example, the ceratopsians *Torosaurus latus* and *Triceratops horridus* have been found in southwestern ND (Pearson et al. 2002), and the hadrosaurids *Edmontosaurus regalis*, *Edmontosaurus annectens*, and ?*Parasaurolophus walkeri* have been identified in the HCF of eastern Montana (Weishampel et al. 2004a). With these and other herbivorous taxa occupying the same river channel–floodplain landscapes, important questions arise as to how these animals interacted with each other and their surrounding environment. Did they compete for plant resources, or did they partition resources by occupying different microhabitats or eating different foods? Answers to these questions not only allow for a better understanding of Mesozoic ecosystems, but they also allow for broad comparisons with mammal behavior during the Cenozoic.

Much of what is known about general dinosaur behavior comes from the study of skeletal morphology, biogeography, and coprolites (Lehman 1987, 2001; Brinkman et al. 1998; Dodson et al. 2004; Horner et al. 2004; Fastovsky and Smith 2004; Chin et al. 1998;

Varricchio 2001). In this paper we use a complementary approach of studying the dietary and habitat preference of animals—stable isotope analyses of fossilized remains. This approach takes advantage of the fact that carbon isotope ratios of C_3 plants and oxygen isotope ratios of surface waters can vary significantly over any given landscape, and that animals record the isotopic characteristics of the part of the landscape they occupy when they ingest organic material and drink from surface water reservoirs (see below). Isotopic studies of modern terrestrial ecosystems (Bocherens et al. 1996), including C_3-only ecosystems (Bocherens 2003; Cerling et al. 2004), indicate that taxonomic offsets among taxa do reflect niche partitioning, and taxonomic offsets observed for ancient C_3 ecosystems have been interpreted in a similar manner (Clementz et al. 2003; MacFadden and Higgens 2004; Botha et al. 2005; Feranec and MacFadden 2006). Therefore it is quite likely that herbivorous dinosaurs preferring open, channel-point bar habitats of the HCF landscape may have different isotopic characteristics than those occupying the canopy or understory of floodplain forests. To test the applicability of this stable isotope approach to studying the behavior of HCF dinosaurs, isotopic comparisons are made among ceratopsians and hadrosaurids from North Dakota, which are in turn compared with carbon isotope data collected from ancient plant material, as represented by bulk sedimentary organic matter. These data indicate that these herbivores had gut physiologies different from those of mammals, and provide evidence for niche partitioning among ceratopsians and hadrosaurids that varied in concert with position on the landscape.

Background: Stable Isotope Ratios, Dinosaurs, and Niche Partitioning

As noted above, carbon isotope ratios of C_3 plants and oxygen isotope ratios of surface waters can vary over any given landscape. Plants using the C_3 (Calvin) pathway presumably dominated Mesozoic ecosystems (Sage and Monson 1999) and are characterized by a large isotopic discrimination between organic

material and CO_2 in the atmosphere. This isotopic discrimination can vary among taxa, with plants such as gymnosperms typically having higher carbon isotope values than others such as ferns (Tieszen 1991; Heaton 1999). Environmental conditions can cause carbon isotope ratios of specific C_3 plants to vary because these ratios are 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. 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; O'Leary et al. 1992; Farquhar et al. 1989; Tieszen 1991). The location of a plant under a closed forest canopy can also affect carbon isotope ratios of plant material, as CO_2 in this setting exhibits lower carbon isotope ratios than the open atmosphere due to plant respiration and decomposition on or near the forest floor (van der Merwe and Medina 1991).

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 the hydrological ''history'' of air masses that are supplying precipitation to these surface water reservoirs (e.g., Epstein and Meyada 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 causes of isotopic variability in surface waters are (1) the preferential incorporation of ^{18}O into condensate as water is precipitated and removed from cooling air masses, and (2) incorporation of ^{16}O into vapor as evaporation of water bodies takes place. 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. Thus, depending on the mix of plants, waters and local environmental conditions, a mosaic of isotopic ''domains'' can exist over any given landscape (Fig. 1), including that associated with the Hell Creek Formation.

Animals living in any given isotopic domain record the isotopic characteristics of it 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. 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 how and which organic compounds are utilized during digestive and metabolic processes (DeNiro and Epstein 1978; Gannes et al. 1998; Hedges 2003; Jim et al. 2004; Passey et al. 2005). 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 (Kohn 1996); thus, it does not influence oxygen isotope *variations* in bioapatite of vertebrates living in different places or drinking different waters. Oxygen isotope ratios of carbonate are, however, more temperature dependent than carbon isotope ratios; thus, variations in animal body temperature are important to consider. For the purposes of this study, it is assumed that dinosaurs utilized carbon in the same basic way as extant vertebrates such as birds, reptiles, and mammals, and that they were homeothermic, regardless of the exact way in which these body temperatures were regulated (e.g., Spotila 1980; Fricke and Rogers 2000; Amiot et al. 2006). It is also assumed *that for a single kind of dinosaur,* controls on the utilization of carbon and oxygen did not vary significantly over time or space.

Because dinosaur bioapatite should provide a record of the ''isotopic systematics'' of the part of the landscape they occupy, isotopic comparisons among populations can be used to address questions of niche partitioning of resources that are otherwise difficult to address using fossil morphology alone. In particular, it is possible to interpret relative differences in isotope ratios among Mesozoic
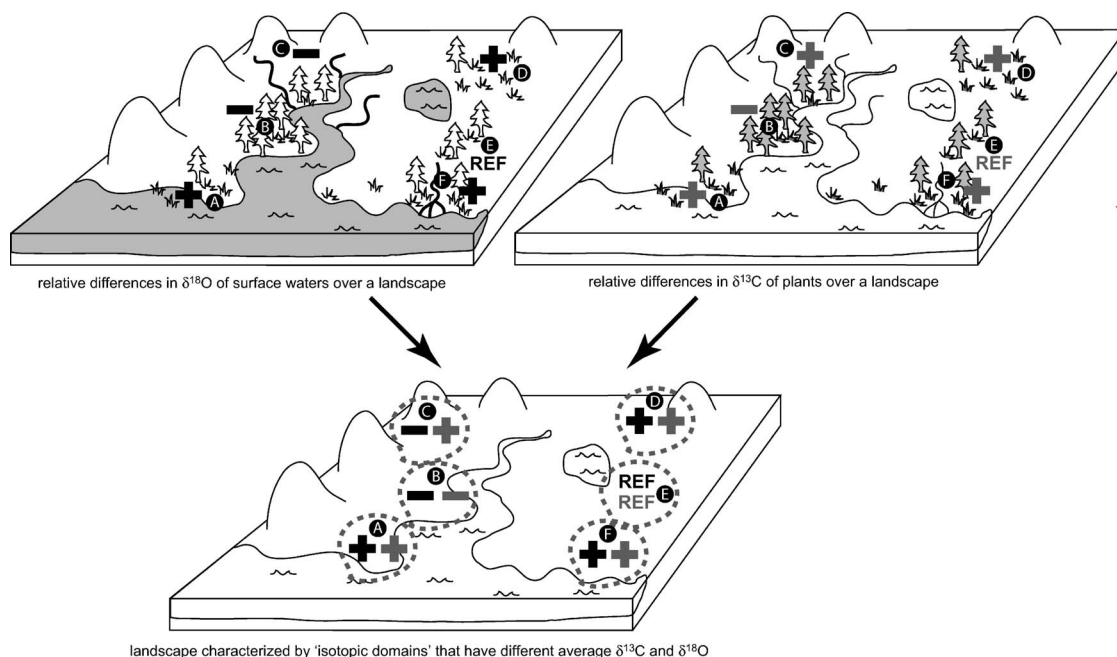
FIGURE 1. Schematic illustration of how different parts of a single C3 ecosystem can be characterized by distinct isotopic domains (after Fricke 2007). These areas include: coastal freshwater swamps (A); riparian forest canopy (B); streams with precipitation from high elevation (C); open shrubland (D); mixed forest/shrubland (E); zone of marine and freshwater mixing (F). Using area E as a baseline, plants living in areas A, C, D, and F are likely to have higher $\delta^{13}C$, while those living in area B are likely to have lower $\delta^{13}C$. Reasons for relatively higher $\delta^{13}C$ 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 $\delta^{13}C$ 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 $\delta^{18}O$, whereas that from B and C is likely to have lower $\delta^{18}O$. Reasons for relatively higher $\delta^{18}O$ 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 $\delta^{18}O$ ocean water with freshwater sourced in precipitation (F). Reasons for relatively lower $\delta^{18}O$ values include reduced evaporation of leaf water in humid, shady, and still understory settings (B) and collection of precipitation from higher elevations having lower $\delta^{18}O$ values (C).

data sets, such as those among taxa from the same locality as reflecting primary (i.e., ancient) isotopic differences in ingested food and water, and thus microhabitat preference. Unfortunately, isotopic *overlap* among taxa is more difficult to interpret; it is possible that these populations each consumed plants and water from different sources where isotope ratios happened to be similar to one other, or that they consumed the same plants and water.

Background: Diagenesis

In order to use stable isotope data to investigate dinosaur ecology, it is important to determine if diagenesis, defined here as the chemical alteration of bioapatite after the death of an animal, obscured original behavioral information. Unfortunately, no method described to date can provide unambiguous evidence whether isotopic alteration has or has not occurred in fossil bioapatite (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 reflected in stable isotope ratios of biogenic apatite. In this case, we feel that by comparing isotopic data (1) between enamel and dentine from the same fossil element, and (2) among vertebrate taxa, and (3) among different microsite localities, 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 general, diagenetic alteration of bioapatite occurs 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 from 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 from 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 from body water, and at temperatures that are much different from 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, whereas 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 are 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 contain <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 and Tuross 2002; Trueman et al. 2004), tooth dentine is less so, and tooth enamel and scale ganoine are least likely to be affected.

For these reasons, enamel is generally considered the best material to analyze in order to obtain primary isotopic information. Nevertheless, anecdotal concerns have been raised that the ''old'' and ''thin'' enamel of dinosaur teeth makes it more prone to interaction with fluids and thus more susceptible to alteration than the ''thick'' enamel of Cenozoic mammals. At present, such concerns are unfounded, as no stable isotope data have been published that demonstrate the existence of temporal or thickness ''thresholds'' at which alteration of enamel becomes problematic. In fact, indirect evidence suggests the opposite. In the case of time, geochemical evidence from trace elements suggests that when diagenesis occurs, it does so thousands to hundreds of thousands of years after burial (Trueman and Tuross 2002; Trueman et al. 2004). Therefore *all* pre-Quaternary fossil material is equally susceptible to diagenetic processes, not just material of Mesozoic age. In the case of thickness, no authors publishing isotopic data from Cenozoic teeth have reported that they discard surface enamel, and thus ''altered'' surface enamel should have negatively affected all such studies. Given the success of stable isotope methods in addressing paleobiological questions, however, such widespread contamination due to altered surface enamel does not appear to be a problem.

Our feeling is that the geologic history of sediments hosting fossilized remains is far more important when considering diagenesis. If there is evidence that sediments have undergone deep burial or have experienced a

great deal of fluid flow (e.g., veins, secondary mineralization), then there is a greater probability that fossils in these sediments may have undergone isotopic modification, regardless of the exact age or type of fossils present. Because the movement of fluids through sediments can vary to a large extent even over small areas, researchers must consider diagenesis on a case-by-case basis using methods such as those described above and those described by Kohn and Cerling (2002), rather than relying on a priori assumptions and arbitrarily defined thickness and age thresholds.

Geologic Setting and Materials

Fossil remains were collected from within the Hell Creek Formation in the general area of Marmarth, North Dakota (Sheehan et al. 1991, 2000; White et al. 1998; Pearson et al. 2001, 2002). The formation is approximately 100 m thick in this area, representing the last ~1.4 Myr of the Maastrichtian Epoch of the Cretaceous Period (Hicks et al. 2002). Vertebrate fossil samples were obtained primarily by surface collection of microsite bonebeds, which typically consist of small resistant elements such as dinosaur and crocodilian teeth, fish scales, and crocodilian and turtle scutes, and which occur as lags associated with channel and crevasse-splay deposits in the part of the HCF investigated here (Pearson et al. 2002). These types of hardpart accumulations, with their great 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). Furthermore, the most taxonomically complete sampling for representation of a paleocommunity is found within channel and nearchannel assemblages because they incise through and most efficiently collect the floodplain deposits (Sheehan et al. 1991; Pearson et al. 2002). Particular fossils collected include shed and fragmentary teeth of hadrosaurian and ceratopsian dinosaurs, although the exact taxonomic identification of shed teeth is difficult to determine. For the study area in general, hadrosaurian remains are indeterminate beyond the family level, whereas the ceratopsians *Torosaurus* and *Triceratops* are the most common identifiable taxa. In addition to teeth, we collected ganoid scales of fish (family Lepisosteidae, referred to as ''gar'' in this paper) as well as multiple samples of bulk sediment. Plant fossils are generally preserved as impressions, and therefore we did not sample leaf cuticle. No authigenic carbonates (e.g., spar, micrite) were found in any of the other sediments or fossils studied, and thus could not be collected.

Sample collection was focused on five separate microsites that are located from 28 to 81 meters below the K/T boundary and within ~50 km of each other (Pearson et al. 2002) (Table 1). Given the limited exposure of outcrop both laterally and stratigraphically that is characteristic of this part of North Dakota, it is not always possible to resolve subtle differences in depositional environment (e.g., channel of a large versus a small river; mud of a lake, floodplain, or swamp) on the basis of sedimentological and paleontological observations from each site. There are no floral localities directly associated with these five microvertebrate localities, which most likely reflects different taphonomic processes for vertebrate hardparts than for more delicate plant remains. It is possible to place the five localities in association with known floral zones that are defined for the HCF in general by the presence and absence of certain plant morphotypes (Johnson 2002) (Table 1), but even these zones are associated with anywhere from 10 to 50 morphotypes. Therefore neither

TABLE 1. Fossil microsite localities sampled as part of this study, as described in Pearson et al. 2002. Meter levels are below the K/T boundary in the areas, and approximate ages were calculated using the sedimentation rates and ages described in Hicks et al. 2002. Although fossil leaves are not found associated with any of these localities, they can be placed in a megafloral zone (Johnson 2002) based on their stratigraphic position.

Site number	Meter level	Age (Ma)	Floral zone
V87006	28.7	65.855	HC II
V86002	28.8	65.86	HC II
V92067	38.9	65.977	HC Ib
V92025	73	66.387	HC Ia
V89004	81.7	66.491	HC Ia

the sediments nor megaflora associated with our vertebrate localities can provide detailed information regarding dinosaur dietary or habitat preferences. Although these limitations deprive us of an independent "tests" of the behavioral interpretations we make below using stable isotope data, they highlight exactly *why* such geochemical data are of value.

Methods and Results

Using a Dremel drill with diamond-tipped bits, we took samples for analysis from dentine and enamel from dinosaur teeth, and dentine and ganoine from gar scales (the latter being homologous to tooth enamel [Zylberberg et al. 1997]). Enamel from ceratopsian teeth is generally thicker than that from hadrosaur teeth and gar ganoine, which ranges from ~0.5 to ~1.5 mm. Enamel and ganoine thickness, however, varies from element to element. Carbon and oxygen isotope ratios of ingested plant matter and water likely varied seasonally by a few per mil (Fricke and O'Neil 1996; Fricke et al. 1998; Sharp and Cerling 1998; Kohn et al. 1998; Straight et al. 2004), and bulk samples of tooth enamel collected from fragmentary material may record only some of this variability. To help overcome this potential problem, we collected and analyzed multiple teeth from each locality. Such sampling of multiple bulk samples allows all the seasonal variability experienced by a single population to be "captured" (Clementz and Koch 2001).

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 $\delta^{13}C$ and $\delta^{18}O$ values, where $\delta = [R_{sample}/(R_{standard} - 1)] \cdot 1000‰$, and the standard is VPDB for carbon and VSMOW for oxygen. $\delta^{18}O$ and $\delta^{13}C$ of tooth enamel carbonate were measured with 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) 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 ±0.1‰ for both $\delta^{18}O$ and $\delta^{13}C$ (1s). 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 0.1M HCl for three hours, rinsed in distilled water four times, and dried. $\delta^{13}C$ was measured on a continuous-flow gas-ratio mass spectrometer (Finnegan Delta PlusXL). Samples were combusted with an elemental analyzer (Costech), which was coupled to the mass spectrometer at the University of Arizona. 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 dinosaur tooth enamel and dentine, and gar scale ganoine and dentine, are given in Appendix 1 (see online supplementary material at http://dx.doi.org/10.1666/08020.s1). Stable isotope data for sedimentary organic material are presented in Appendix 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. We used Microsoft Excel for these statistical analyses, as well as for determining correlation coefficients. Carbon and oxygen isotopic comparisons were made (1) between enamel/ganoine and dentine from the same type of animal from each horizon; (2) between enamel and ganoine from coexisting ceratopsians, hadrosaurs, and gar at each locality; and (3) between enamel and ganoine from ceratopsians, hadrosaurs, and gar grouped by inferred environmental preference (see below). Results are summarized in Appendix 3.

Discussion

Comparisons of isotopic data obtained from enamel, ganoine, dentine, and organic material can be used to address questions regarding diagenesis, dinosaur physiology and dinosaur behavior. Each of these topics is discussed in more detail below.

Diagenesis.—In an effort to demonstrate that

diagenesis has not entirely obscured original behavioral information that is reflected in stable isotope ratios of bioapatite, comparisons of isotopic data are made (1) between enamel and dentine from the same fossil element, (2) among vertebrate taxa, and (3) among different microsite localities.

As noted above, the rationale behind a comparison of isotopic data from enamel and dentine is that isotope ratios of dentine should represent a more diagenetically altered material. Thus isotopic differences between dentine and enamel can be used to address the preservation of the latter. In general, dentine is characterized by higher $\delta^{18}O$ and $\delta^{13}C$, particularly carbon isotope ratios, relative to enamel (Fig. 2); lines drawn between average values can illustrate these relations more clearly (solid lines; Fig. 2). Assuming unaltered enamel and dentine of teeth had the same isotope ratios, the trend in dentine toward higher isotope ratios is interpreted to represent a variable exposure of dentine to diagenetic fluids, more isotopic exchange, and/or secondary mineral formation in dentine compared to enamel, and thus isotope ratios closer to the diagenetic end-member (which in this area must be characterized by moderately high $\delta^{18}O$ and very high $\delta^{13}C$). It is important 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. 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. Overall, these general isotopic differences between enamel and dentine indicate that original ranges in $\delta^{18}O$ and $\delta^{13}C$ of enamel were not modified to the same degree as for dentine,

and thus diagenetic alteration of enamel is minimal.

Comparisons of enamel-ganoine data only among HCF taxa provide more convincing evidence for limited effect of diagenesis on enamel isotope ratios. In particular (1) significant offsets in average $\delta^{18}O$ and/or $\delta^{13}C$ are observed between at least two taxa from every microsite, (2) different correlation coefficients for $\delta^{18}O$ and $\delta^{13}C$ are observed for coexisting taxa, and (3) intra-populational variance in $\delta^{18}O$ and $\delta^{13}C$ is different for coexisting taxa (Fig. 3). Similar kinds of taxonomic differences in average $\delta^{18}O$ and/or $\delta^{13}C$, and in isotopic variance, have been observed in studies of modern and Cenozoic mammalian tooth enamel (Bocherens et al. 1996; Bocherens 2003; Clementz et al. 2003, 2006; Cerling et al. 2004; MacFadden and Higgins 2004; Feranec and MacFadden 2006), and they have been interpreted to reflect physiological and/or ecological differences among taxa. They are not unexpected in Mesozoic ecosystems because although enamel of hadrosaurian and ceratopsian teeth and ganoine of gar scales are mineralogically and structurally similar, the animals are characterized by different physiologies and/or ecological behaviors.

The simple observation that offsets in average $\delta^{18}O$ and/or $\delta^{13}C$ and different correlation coefficients are preserved among taxa is strong evidence that any isotopic exchange between groundwaters and enamel-ganoine or secondary precipitation of carbonate in enamel-ganoine was not extensive enough to obscure original paleoecological and paleobiological information. If diagenetic alteration was a significant occurrence, then the result should be uniform isotope ratios, similar correlation coefficients, and similar variances for all remains in a single microfossil bonebed, *regardless* of taxonomic affinity. It should be noted that it is not necessary to have an a priori understanding of the exact physiological/ecological meaning of these taxonomic offsets in order for them to be useful in addressing the issue of diagenetic alteration (although specific physiological and ecological interpretations of these offsets are provided below). It is simply enough to know that isotopic offsets and differences in correlation coefficients among
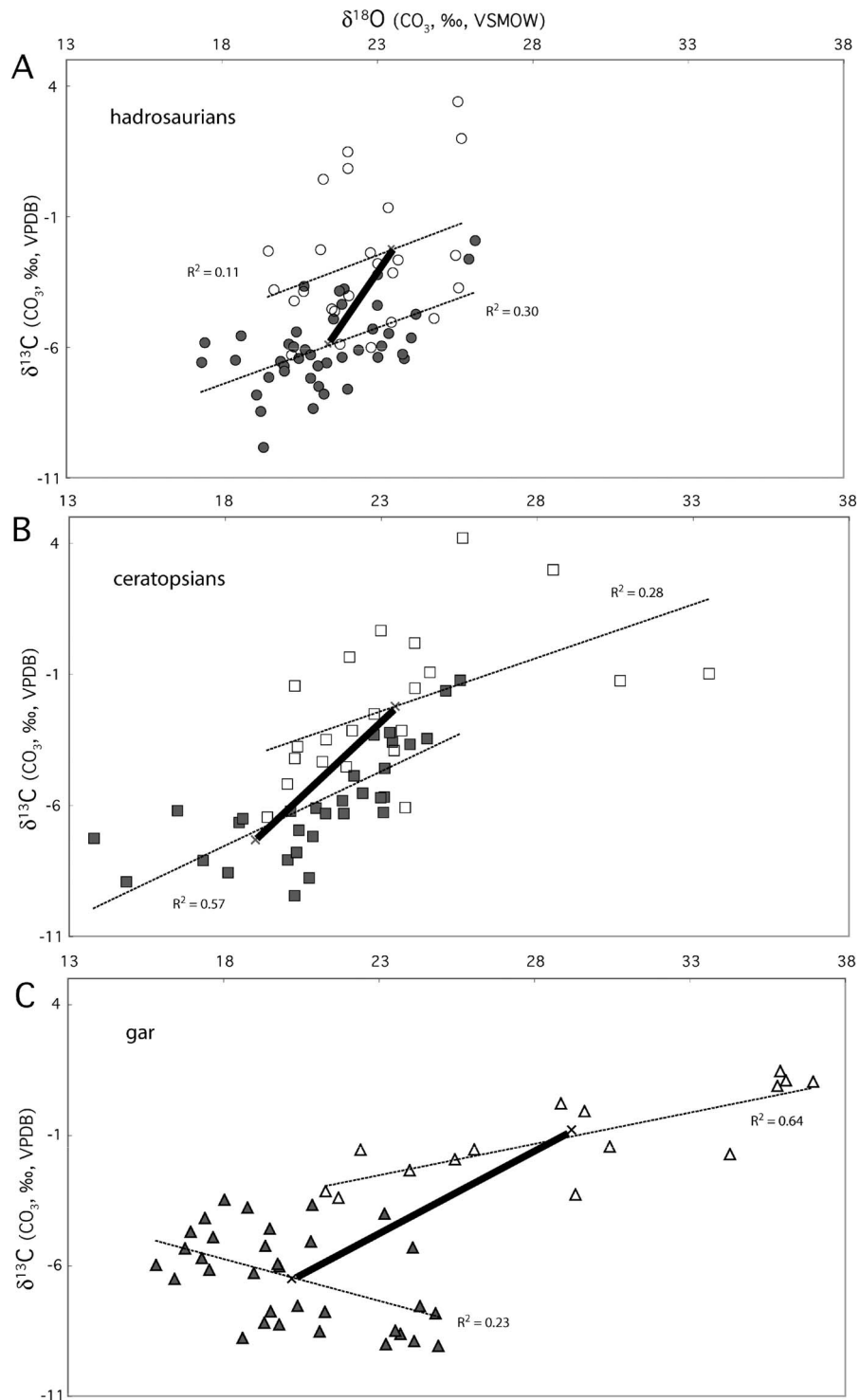
FIGURE 2. Comparisons of isotope data from enamel-ganoine (closed symbols) and dentine (open symbols) for hadrosaurians (A), ceratopsians, (B) and gar (C). Regression lines are dashed and average isotope ratios are shown with an ''×.'' In all cases, dentine is characterized by higher carbon-to-oxygen isotope ratios. 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. Solid lines connecting average isotope ratios for enamel-ganoine and dentine illustrate the general isotopic trends characteristic of diagenetic alteration.
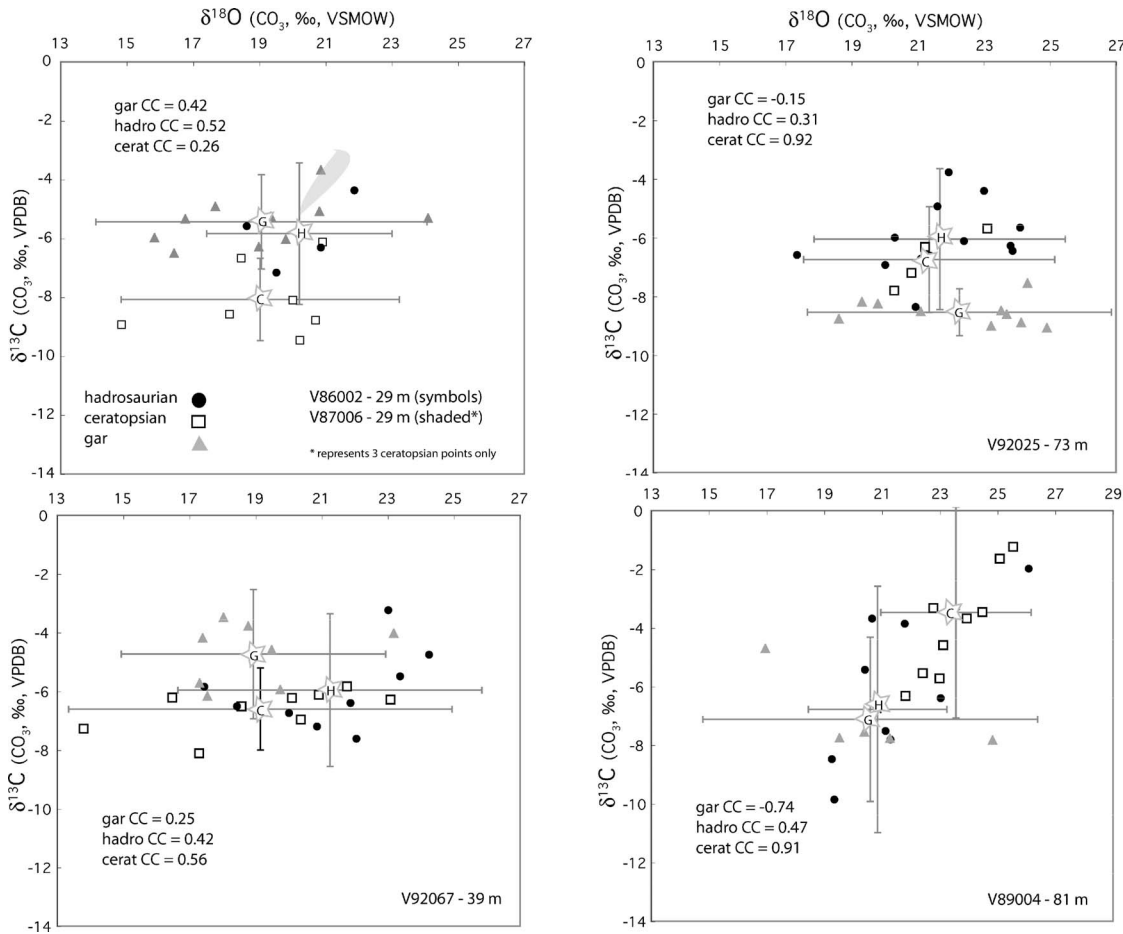
FIGURE 3.   Isotopic differences among enamel and ganoine of coexisting ceratopsians, hadrosaurs, and gar from four microsites. Average isotope ratios are represented by a star and the corresponding initial for each animal (C, H, G), and isotopic variability is represented by ±2σ uncertainty bars. Correlation coefficients (CC) are also provided for each taxon. Limited ceratopsian data from site V87006 (shaded area) are included along with data from the nearby site V86002. Level below the K/T is given in meters for each site. Extensive overprinting of primary isotope signals by diagenetic carbonate should result in uniform isotope ratios. Thus, the within-site differences in averages and isotopic variability, and in correlation coefficients, are evidence that complete isotopic resetting did not occur. Note that in the case of site V89004, a single hadrosaurian enamel sample had anomalously high isotope ratios compared to other hadrosaurians, but falls within the range for ceratopsians. This sample may be a ceratopsian tooth that was incorrectly identified, and it is not included in the average and uncertainty calculations for hadrosaurian data.

animals can be preserved only if isotopic alteration does not obscure original isotopic information. It should also be noted that isotopic overlap that is observed among taxa at each site does not necessarily imply diagenetic alteration; instead these particular animals could have consumed plants and water from different sources where isotope ratios happened to be similar to one other, or they could have fractionated carbon and oxygen in different ways that happened to result in similar $\delta^{18}O$ and $\delta^{13}C$ of bioapatite.

The last critical observation to make regarding diagenesis is that offsets in average $\delta^{18}O$ and/or $\delta^{13}C$, correlation coefficients, and isotopic variances among taxa are not the same for each microsite; rather two basic offset patterns can be observed. In one, composed of samples from V86002 (29 m) and V92067 (39 m), gar ganoine has the highest mean $\delta^{13}C$ of all taxa and ceratopsian enamel has the lowest mean $\delta^{13}C$ and $\delta^{18}O$ values and these data are characterized by a low correlation coefficient (Fig. 4A). In contrast, the general pattern for
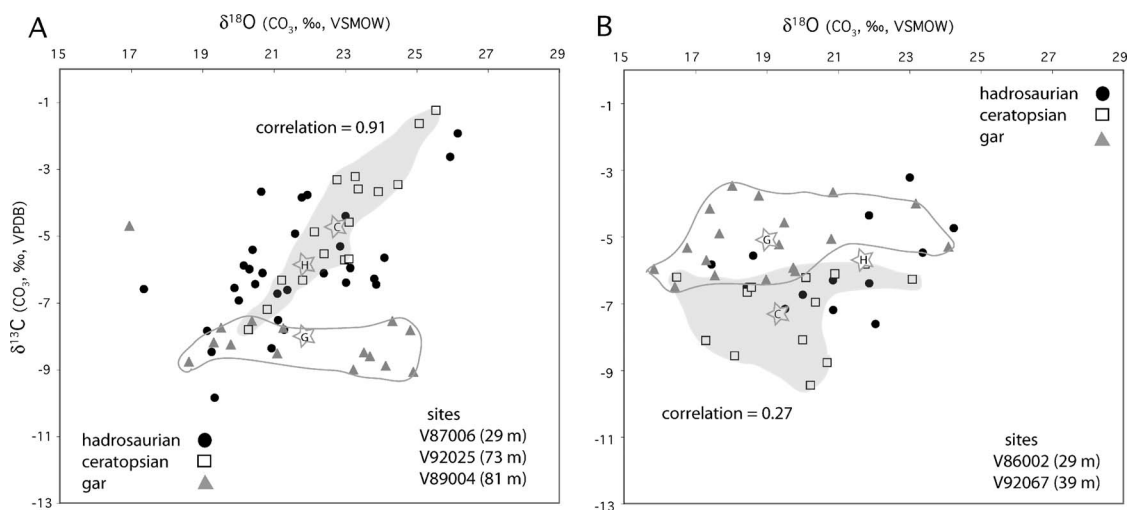
FIGURE 4. Two distinct groupings of stable isotope data for ceratopsians, hadrosaurs, and gar from the five sampled microsites. Average isotope ratios for each grouping are represented by a star and the corresponding initial for each animal (C, H, G). Level below the K/T is given in meters for each site. In one group (A), ceratopsians have higher $\delta^{18}O$ and $\delta^{13}C$ than associated gar, as well as a high correlation coefficient (0.91). In the other (B), ceratopsians have lower $\delta^{13}C$ than associated gar, and a low correlation coefficient (0.27). It is difficult, if not impossible, to provide a plausible diagenetic scenario to explain differential fluid flow that could preserve isotopic differences among taxa, yet cause a change in direction and nature of these differences for sites from the same formation located so close to each other.

sites V87006 (29 m), V92025 (73 m), and V89004 (81 m) consists of gar ganoine with the *lowest* mean $\delta^{13}C$ of all taxa and ceratopsian enamel with the *highest* mean $\delta^{13}C$ and $\delta^{18}O$ values (Fig. 4B). Furthermore, there is a strong covariation between $\delta^{18}O$ and $\delta^{13}C$ for these ceratopsians. All of the sampled microsites are relatively close together, separated stratigraphically by less than ~50 m, and separated laterally by less than ~50 km. In particular, sites V86002 and V87006 are within a meter of each other from the same outcrop area (Pearson et al. 2002). It is difficult, if not impossible, to provide a plausible diagenetic scenario to explain differential fluid flow that could preserve isotopic differences among taxa, yet cause a change in direction and nature of these differences for sites from the same formation located so close to each other. Instead, it is more likely that original paleoecological information is preserved, and that these two patterns accurately represent the environments or behaviors of animals, which were in fact different (see below).

To summarize this discussion of diagenesis, we admit that any one of the isotopic comparisons described above does not provide conclusive evidence that original paleoenvironmental, paleoecological, and/or paleobiological information is retained in enamel-ganoine isotope data. However, when isotopic offsets from all materials, from all taxa, and from all microsites 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.

High Carbon Isotope Ratios.—It has been noted in other studies of Late Cretaceous herbivorous dinosaurs, in particular hadrosaurs, that $\delta^{13}C$ values are unusually 'high' when considered in the context of data from mammals living in C_3 ecosystems (Stanton-Thomas and Carlson 2003; Fricke et al. 2008), and this could be due in part to diagenetic processes (Stanton-Thomas and Carlson 2003). In an effort to determine whether diagenesis is a possible reason for these higher values in spite of arguments such as those made above, Fricke et al. (2008) compared $\delta^{13}C$ of hadrosaur tooth enamel from two Campanian-aged sites with $\delta^{13}C$ of associated sedimentary organic matter and paleosol carbonate nodules with the goal of estimating the carbon isotope offset be-
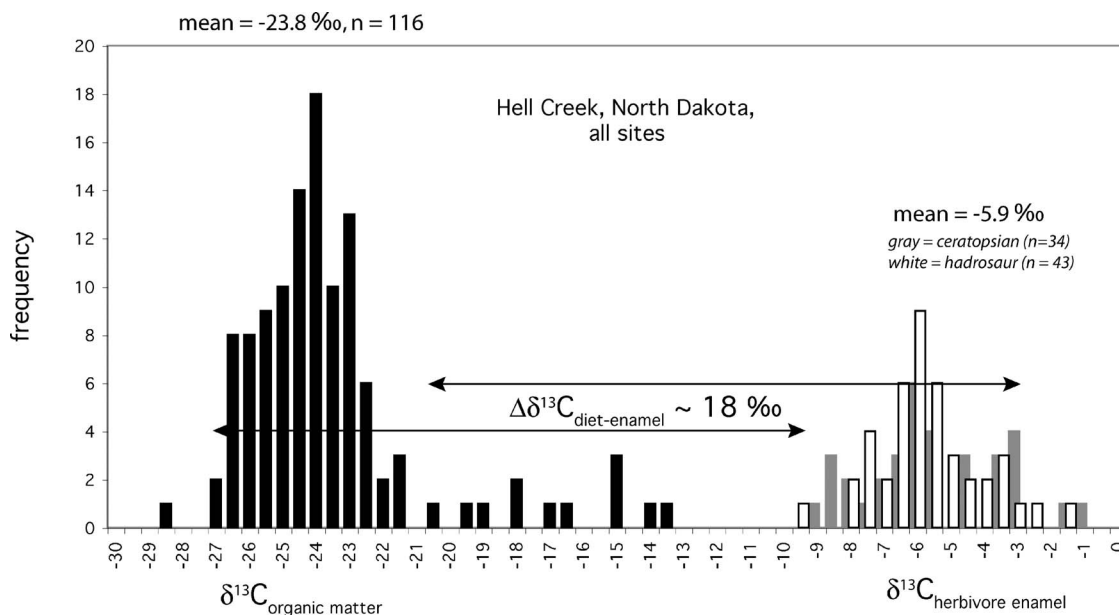
FIGURE 5. $\delta^{13}C$ of herbivore tooth enamel and $\delta^{13}C$ of bulk sedimentary organic matter collected from sediments associated with microfossil bonebeds of the Hell Creek Formations. The range in $\delta^{13}C$ of HCF organic matter is similar to that of modern C3 plants, although absolute values are several per mil higher than modern values in part because $\delta^{13}C$ of atmospheric CO_2 was higher during the Late Cretaceous. The average offset between enamel and presumed diet is ~18‰. This same offset exists regardless of exact age, location, depositional environment, or herbivore species (see also Fricke et al. 2008), and suggests that herbivorous dinosaurs utilized organic carbon in a manner different than modern mammals.

tween diet and tooth enamel ($\Delta\delta^{13}C_{\text{diet-enamel}}$). They concluded that $\Delta\delta^{13}C_{\text{diet-enamel}}$ was ~18‰, which is in fact larger than the ~12 to 15‰ observed for modern mammals (Koch 1998; Cerling and Harris 1999; Kohn and Cerling 2002; Hoppe et al. 2004; Passey et al. 2005), a conclusion supported by isotopic data from HCF sediments studied here (Fig. 5). Altogether, herbivorous dinosaur material and associated organic matter from 8 other microfossil bonebeds ranging in age from late Campanian to late Maastrichtian and in space from western Montana to western North Dakota has been analyzed, and the average $\Delta\delta^{13}C_{\text{diet-enamel}}$ is always ~18‰ (Fricke et al. 2008: Fig. 5). Such remarkable consistency indicates that the observed $\Delta\delta^{13}C_{\text{diet-enamel}}$ for dinosaurs is a primary signal, as the possibility of 'convergent diagenesis' leading to similar offsets despite differences in time and geographic location is highly unlikely. Therefore carbon isotope systematics of modern mammals do not appear to provide a valid context for interpreting data from dinosaurs, and 'high' $\delta^{13}C$ values of tooth enamel alone

should not be considered as evidence for intense diagenetic alteration of primary signatures.

Reasons for a larger $\Delta\delta^{13}C_{\text{diet-enamel}}$ for herbivorous dinosaurs of this study compared to modern mammals are likely due to 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). These factors are thought to explain the observations that $\Delta\delta^{13}C_{\text{diet-enamel}}$ is actually variable for large mammalian herbivores themselves, ranging from ~12‰ to 15‰ (Koch 1998; Cerling and Harris 1999; Kohn and Cerling 2002; Hoppe et al. 2004; Passey et al. 2005), and that $\Delta\delta^{13}C_{\text{diet-eggshell}}$ for birds is even greater (~16‰; Johnson et al. 1998). Thus it is possible that hadrosaurs and ceratopsians 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 led to a larger $\Delta\delta^{13}C_{\text{diet-enamel}}$. Such implied differences in dinosaur gut biology implied by a larger offset could in turn explain the apparent ability of hadrosaurs and ceratopsians to get adequate nutrition from low-quality, fibrous plant material thought to be available to them (e.g., Dodson et al. 2004; Fastovsky and Smith 2004; Horner et al. 2004). Although not the main focus of this study, the paleobiological implications of these results are intriguing and are the focus of ongoing research.

Partitioning of Hell Creek Habitats among Dinosaurs.—Isotopic offsets between ceratopsian and hadrosaurid tooth enamel (and between dinosaurs and gar) occur at all stratigraphic levels, although the nature of these offsets, as well as patterns in ceratopsian data, differs from site to site (Figs. 3, 4). Because oxygen and carbon in bioapatite have a source in ingested water and food, respectively, these isotopic patterns do not represent random patterns influenced by depositional environments or taphonomic processes; rather, at the most basic level these offsets must reflect either physiological or ecological differences among coexisting animals.

Considering dinosaurs only, different average body temperatures could affect isotopic fractionation of oxygen during bioapatite formation, whereas differences in how organic carbon is utilized could affect carbon isotope ratios of enamel carbonate. It is unlikely, however, that such physiological factors can account for the observed taxonomic offsets. First, hadrosaurs have relatively constant $\delta^{18}O$ and $\delta^{13}C$ values throughout the section, indicating that any physiological changes for this taxon were minimal. In contrast, average $\delta^{18}O$ of ceratopsians ranges from $\sim-8\permil$ to $\sim-12\permil$, and this in turn would require body temperatures of ceratopsian populations to vary up to $\sim16°C$. It has been suggested that large dinosaurs such as ceratopsians were likely effective homeotherms because of their large body mass (e.g., Spotila 1980) or because of endothermic metabolic activity (Fricke and Rogers 2000; Amiot et al. 2006); thus, such

large physiological differences among ceratopsian species are implausible. In the case of carbon, average $\delta^{13}C$ of ceratopsians range from $\sim-9\permil$ to $\sim-6\permil$, and these changes in $\delta^{13}C$ of ceratopsians would imply a dramatic change in organic carbon utilization among related species that is much larger than differences in $\Delta\delta^{13}C_{\text{diet-enamel}}$ observed among taxa even at the order level in modern mammals (Cerling and Harris 1999; Passey at al. 2005). For these reasons, the observed isotopic offsets among taxa must be primarily consequences of behavioral differences among hadrosaurs and ceratopsians.

Because differences in $\delta^{13}C$ and $\delta^{18}O$ of tooth enamel carbonate are assumed to reflect $\delta^{13}C$ and $\delta^{18}O$ of ingested plants and surface waters, respectively, the most parsimonious interpretation of dinosaur data is that hadrosaurs and ceratopsians were utilizing different microhabitats that made up the Hell Creek ecosystem. What is especially interesting is that the isotopic systematics, and thus habitat preferences, of ceratopsians appears to vary over time. As illustrated in Figure 4, ceratopsians from sites V89004 (81 m), V92025 (73 m), and V87006 (28 m) have higher $\delta^{13}C$ and $\delta^{18}O$ values with a high correlation coefficient relative to hadrosaurs, whereas ceratopsians from sites V92067 (39 m) and V86002 (29 m) have lower $\delta^{13}C$ and $\delta^{18}O$ than associated hadrosaurs. The nature of these habitat preferences, and how they may have changed over time, can be inferred from relative differences in isotope ratios and their patterns for each taxa combined with general sedimentological and paleobotanical observations from the HCF (as noted above it is not possible to provide independent sedimentological and paleobotanical evidence to support these interpretations on a microsite-by-microsite basis).

In the case of sites V89004, V92025, and V87006, higher $\delta^{18}O$ and $\delta^{13}C$ and a high correlation coefficient (0.91) for ceratopsians are thought to reflect their preference for drinking and feeding in open habitats—channel bars of large rivers, swamps, tidal flats—that may have had some connection to the marine environment (Fig. 6, lower box). Sedimentological data indicate that such settings were characteristic of the HCF in general (Fastovsky
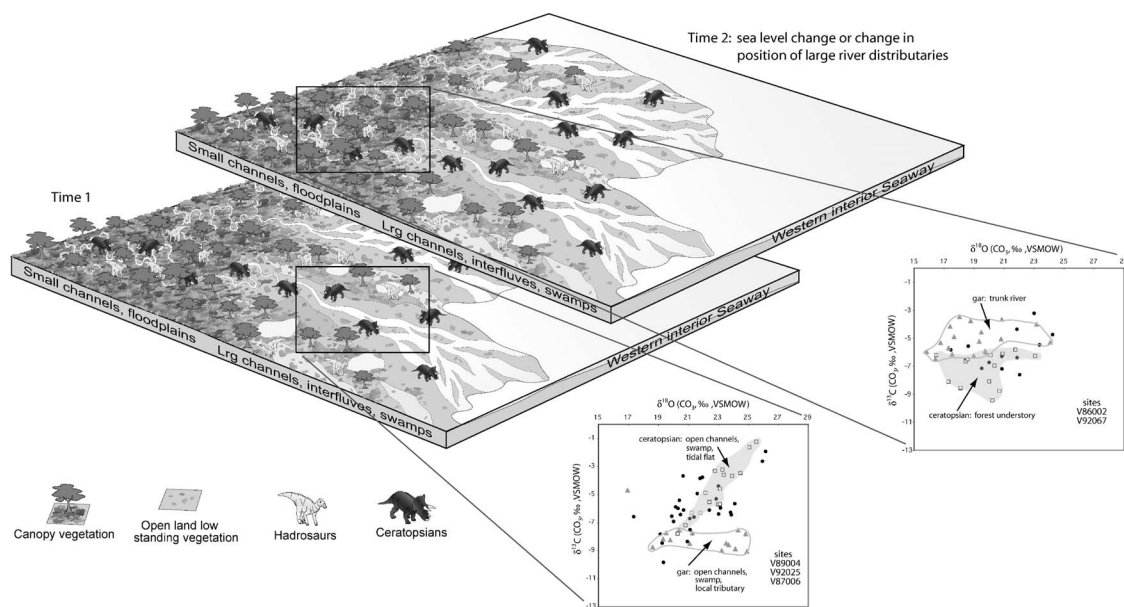
FIGURE 6. Schematic illustration of the Hell Creek landscape, the environments occupied by dinosaurs and fish that account for isotopic patterns illustrated in Figure 4, and how the location of these environments could shift over time. For both times 1 and 2, areas closer to the shoreline have a mix of vegetation types in the river channels, riparian forests, freshwater swamps, and tidal marshes. Because of their location relative to the coast, these areas can have a hydrological connection with the marine environment as well as with local precipitation. Farther inland, meandering trunk rivers are associated primarily with forested areas only. Rivers have a hydrological connection with upland drainages as well as local precipitation. The inferred relations between these two general kinds of environments and herbivore behavior are highlighted by the upper and lower boxes, which are linked to grouped isotopic data from Figure 4. Stratigraphic-temporal changes in environments, and thus isotopic patterns, can be explained by changes in sea level, and hence the position of the shoreline, and/or by changes in the position of rivers and associated distributary networks over time (such as those represented here by the landscape reconstructions for times 1 and 2).

1987; Hartman and Kirtland 2002; Murphy et al. 2002; Pearson et al. 2002), and paleobotanical data indicate that sediment bars of large open river systems of the HCF were characterized by a shrubby and herbaceous flora different from that of floodplain forests (Johnson 2002). Lacking a forest canopy, plants in these settings, as well as those living in other coastal settings such as tidal marshes or swamps, could have been more susceptible to evaporative loss of water from ponds, soils, or leaves, which would shift $\delta^{18}O$ of these waters to higher values (Sternberg 1989; Gat 1996). Ocean water typically has much higher $\delta^{18}O$ than precipitation even in coastal areas (Rozanski et al. 1993; Gat 1996), and so a mixing of precipitation and ocean water in coastal areas could also result in brackish surface waters with higher $\delta^{18}O$ values. Evidence that surface waters with a wide range in $\delta^{18}O$ did in fact exist for ceratopsians to drink from is provid-

ed by the range in $\delta^{18}O$ of gar for these sites (Fig. 4A), which is similar to that observed for ceratopsians. In the case of carbon, marine influences and open coastal settings can also result in higher $\delta^{13}C$ of C_3 plants. For example, coastal mangroves affected by salt and nutrient stress today have $\delta^{13}C$ values up to 5‰ higher than those that are not (McKee et al. 2002; Wooller et al. 2003), an effect also observed for Cretaceous plant fossils of the same order as those found in the HCF (Nguyen Tu et al. 1999; Aucour et al. 2008). Furthermore, leaves of C_3 plants exposed to direct sunlight, such as would be found in more open settings, typically have $\delta^{13}C$ values that are 2–3‰ higher than those that are not (Lockheart et al. 1998). Lastly, aquatic vegetation growing in ocean waters typically has higher $\delta^{13}C$ values than land and aquatic vegetation from terrestrial settings (Boutton 1991; summary in Clementz and Koch 2001). Because both $\delta^{18}O$ of

surface waters and $\delta^{13}C$ of plants increase in response to more open and marine-influenced conditions, a positive correlation between them, such as that observed for ceratopsians (Fig. 4A), is expected.

In contrast, lower $\delta^{18}O$ and $\delta^{13}C$ values of hadrosaurs from V89004, V92025, and V87006 (Fig. 4A) indicate that these animals preferred a microhabitat different from that of coexisting ceratopsians, in particular river and floodplain forests. Again, sedimentological data indicate that such depositional environments were common on HCF landscape (Fastovsky 1987; Murphy et al. 2002), and paleobotanical data indicate associated that forests were made up of small to medium-sized trees (Johnson 2002). Lower $\delta^{18}O$ and $\delta^{13}C$ values suggest that these forests were not influenced by marine waters and were characterized by more dense vegetative cover (''fingers'' of interfluve vegetation in Figure 6). Nevertheless, the weak covariation in $\delta^{18}O$ and $\delta^{13}C$ implies that C_3 plants in this habitat experienced a range of environmental conditions, perhaps from more humid, shady understory (lower $\delta^{18}O$ and $\delta^{13}C$) to a more exposed canopy top where water loss via transpiration was more likely (higher $\delta^{18}O$ and $\delta^{13}C$). Overall, these taxonomic differences in isotope ratios among ceratopsians and hadrosaurs from V89004, V92025, and V87006 are indicative of a spatial, or *horizontal*, partitioning of food resources from adjacent areas characterized by different types of marsh, swamp, and forested vegetation (Fig. 6). This interpretation is consistent with the biogeographic distribution of ceratopsian remains, which suggest that these animals preferentially occupied coastal marshes and swamps (Lehman 1987, 2001; Brinkman et al. 1998)

Focusing now on sites V92067 and V86002, evidence for dietary niche partitioning is still quite evident, but the nature of this partitioning is different than for the other sites. In these cases, ceratopsians generally have lower $\delta^{18}O$ and $\delta^{13}C$ values than coexisting hadrosaurs (Fig. 4B), whose average isotope ratios remain relatively unchanged with stratigraphic position (Fig. 4). Because hadrosaurs show this isotopic consistency, we infer that they occupied a similar river-floodplain forest microhabitat. Lower $\delta^{18}O$ and $\delta^{13}C$ values for ceratopsians suggest that they also occupied such a closed-forest setting; however, they relied on water and plant resources from the understory of this forest rather than from the canopy (Fig. 6 upper box). In the case of modern closed-canopy forests located in tropical regions, $\delta^{13}C$ of C_3 plants varies by up to 10‰ depending on the plant's position in the canopy, with lower plants having lower $\delta^{13}C$ due to recycling of CO_2 or to more humid, shaded conditions (van der Merwe and Medina 1991; von Fisher and Tieszen 1995; Martinelli et al. 1998; Cerling et al. 2004). This pattern in $\delta^{13}C$ of C_3 plants is mirrored by herbivores, with those feeding preferentially in the understory having lower $\delta^{13}C$ of tooth enamel (Cerling et al. 2004). Furthermore, herbivores occupying understory microhabitats are also characterized by lower $\delta^{18}O$ compared to those utilizing canopy plants (Cerling et al. 2004), presumably because evaporation of water is reduced by higher humidity and more shade. Overall, taxonomic differences in isotope ratios among ceratopsians and hadrosaurs are again indicative of a partitioning of food resources, only in this case it is a *vertical* partitioning within the same area (Fig. 6), rather than a horizontal partitioning between adjacent areas. This interpretation is consistent with previous morphological studies of these dinosaurs, which suggest that in forested settings the size and orientation of ceratopsian skeletons would have led to a preference for understory (~1–2 m) vegetation, whereas hadrosaurs would have browsed at low to intermediate heights (2–4 m) (Dodson et al. 2004; Horner et al. 2004; Fastovsky and Smith 2004).

Relation of Niche Partitioning, Available Vegetation, and Landscape Change.—The change in isotopic offsets and thus ceratopsian diet over time described above begs the question of the cause of this change in behavior. The most obvious answer is that the behavior of ceratopsians simply reflects the type of vegetation available to them in any one part of the Hell Creek landscape. Reasons for a change in the type of vegetation present in any one place include sea level rise or fall, and/or a change in the position of river channels and networks of deltaic distributaries. Even a small change in

sea level would result in a broad migration of depositional environments either landward or seaward over this broad shallow landscape, and this in turn determines the location of open tidal marshes, wide river channels, and connection to marine water (times 1 and 2; Fig. 6). Alternatively, a change in the position of river channels and associated landforms such as deltas and distributaries could produce a similar change in vegetation types in the absence of a change in sea level (times 1 and 2; Fig. 6).

Sedimentological and paleontological evidence for such subtle, and apparently short-lived, variations in depositional environment is difficult to obtain in our field area; nevertheless, isotopic data from gar scales are consistent with their existence. Just as for terrestrial vertebrates, isotopic ratios of gar scales reflect those of ingested water and food, and a large difference in $\delta^{18}O$, and particularly $\delta^{13}C$, for gar between sites V89004-V92025-V87006 and sites V92067-V86002 (Fig. 4) indicates that these animals lived in different settings. In particular, higher $\delta^{18}O$ and lower $\delta^{13}C$ values from V89004-V92025-V87006 are suggestive of local precipitation, perhaps modified by evaporation and ocean mixing, as a source of water, and local organic matter as a source of carbon in the rivers and swamps that were likely occupied by these fish (Fig. 6 lower box). In contrast, lower $\delta^{18}O$ and higher $\delta^{13}C$ for gar from V92067-V86002 indicate that water there had a source in precipitation from higher elevation areas and a contribution of carbon from the dissolution of marine carbonates, both of which are consistent with these fish living in meandering trunk streams with a direct hydrologic connection to upland areas (Fig. 6, upper box). It is interesting to note that the $\delta^{18}O$ of river water inferred to be in equilibrium with gar bioapatite at 10°C (average mean annual temperature [MAT] for time studied time interval [Wilf et al. 2003]) ranges from $\sim-16‰$ to $-7‰$ for all sites, and this is similar to the range in $\delta^{18}O$ of river waters inferred from $\delta^{18}O$ of bivalves shells collected from HCF localities in Montana (Dettman and Lohmann 2000).

Limits of Taxonomic Resolution.—Because of our inability to identify shed teeth beyond the family level, isotopic data from this study can be used only to delineate broad dietary differences and habitat preferences among hadrosaurian and ceratopsian dinosaurs. Therefore, it is possible that individual dinosaur species had dietary or habitat preferences that we are not able to distinguish with these data. For example, the hypothesized change in ceratopsian dietary preference with environment does not require that a single ceratopsian taxon underwent a change in behavior; rather it could be that different genera or species may be present during each specific time period, each with its own unique behavior patterns. In fact, two ceratopsian genera, *Torosaurus* and *Triceratops* are found in HCF in this area, and on the basis of biogeographic distributions Lehman (1987) suggested that *Triceratops* preferred tidal marsh/swamp settings more than *Torosaurus*, and would thus be the more common taxon in a setting such as those inferred for sites V89004-V92025-V87006. In the case of hadrosaurs, it is not possible to determine if a single species with a generalist behavior is associated with the entire range in isotope ratios, or whether multiple species with unique dietary preferences and smaller isotopic ranges are instead grouped together. Future stable isotope research involving identifiable specimens is required to test these possibilities.

Summary

This study provides the first direct geochemical evidence for dietary niche partitioning among coexisting herbivorous dinosaurs, specifically ceratopsians and hadrosaurs. Furthermore, changes in isotopic offsets among these taxa suggest that the nature of this niche partitioning varies in response to changes in vegetation structure, with ceratopsians preferring open marsh settings when they are present along with forests, but preferring understory vegetation in forest-only environments. The interpretations of stable isotope data presented here are consistent with ceratopsian and hadrosaur behaviors inferred from morphological characteristics of these dinosaurs, and demonstrate the potential of stable isotope studies to (1) complement other kinds of paleontological research, and (2) provide novel information regarding late Cretaceous

plant-animal interactions, resource partitioning among herbivores, and vertebrate community structure as a whole. The ability of stable isotope data to reveal behavioral differences among herbivorous dinosaurs, even in the face of low taxonomic resolution, bodes well for the use of this approach in areas with fossils that can be identified to the genus or species level.

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