

Variations in hadrosaurid behavior, soil processes, and forest structure over
the Late Cretaceous landscape of southern Utah (Kaiparowits Formation,
Grand Staircase Escalante National Monument)

A Thesis

Presented to

The Faculty of the Department of Geology

The Colorado College

In Partial Fulfillment of the Requirements for the Degree

Bachelor of Arts

By

Victoria F. Crystal

May 2014

On my honor, I present this thesis for distinction to the Faculty of the Department of Geology of The Colorado College as my own work in accordance with the Colorado College Honor Code.

Victoria F. Crystal, May 2014

Table of Contents

List of Figures	iv
List of Tables	v
Abstract	1
1. Introduction	3
2. Background	8
<i>2.1 Stable isotope ratios and past environments</i>	8
<i>2.1.1 Isotopic variations in plants and water over a landscape</i>	8
<i>2.1.2 Vertebrate tooth enamel as a record of plant and water isotope ratios</i>	9
<i>2.1.3 Isotope ratios of tooth dentine as a record of soil processes</i> ...	10
3. Methods	13
4. Results	15
5. Discussion	16
<i>5.1 Diagenesis and preservation of primary ecological information in hadrosaurid tooth enamel</i>	16
<i>5.2 Enamel isotope ratios and hadrosaurid niche partitioning</i>	19
<i>5.3 Landscape variability in redox conditions and methane production</i>	26
<i>5.4 Implications of evidence for methane production along the coast of the KWIS</i>	27
<i>5.4.1 Impact of methane production on Late Cretaceous climate</i> ... 27	
<i>5.4.2 Methane production and forest structure of the Kaiparowits landscape</i>	29
6. Conclusion	32
Acknowledgements	36
References	37

List of Figures

Figure 1: Late Cretaceous North America.....	6
Figure 2: Location of sample localities.....	7
Figure 3: Hadrosaurid enamel and dentine	17
Figure 4: Hadrosaurid enamel and dentine by locality	18
Figure 5: Hadrosaurid enamel.....	20
Figure 6: Interpretation of paleoenvironments.....	25
Figure 7: Hadrosaurid Dentine.....	28
Figure 8: Oxidation of organic matter.....	30
Figure 9: Methanogenesis.....	31

List of Tables

Table 1: Stable isotope ratios for hadrosaurid enamel and dentine for the Kaiparowits Formation.....	34
Table 2: Results of statistical analyses.....	35

Abstract

During the Late Cretaceous, western North America was flooded by an inland sea, the coasts of which were covered by broad, low-relief fluvial/alluvial plains on which a wide variety of dinosaurs and plants lived. Although these “actors” are known, their “actions” are not as clear; in particular, details of surface processes, dinosaur behavior and forest structure are not known for certain. In this study, stable isotopes of fossilized teeth from hadrosaurid dinosaurs collected in two different areas within the Kaiparowits Formation are used to investigate possible surface methane production, dinosaur niche partitioning, and the nature of the forest canopies in southern Utah during the Late Cretaceous to answer some of these outstanding questions.

Comparison of carbon isotope ratios of tooth enamel between the two areas reveals significant offsets, which can be explained by differences between the areas in either (1) plant communities, (2) environmental and climatic stressors, or (3) the cycling of carbon within a forest canopy. Regardless of the exact cause, the preservation of these differences in hadrosaurid tooth enamel provides evidence of dietary niche partitioning amongst hadrosaurid sub-families within low-lying fluvial environments in southern Utah during the Late Cretaceous.

Significant differences in both means and ranges of carbon isotope ratios of tooth dentine also exist between areas. Unlike enamel, dentine does not preserve primary isotopic information; rather, its chemical composition is strongly influenced by chemical processes taking place in soils near the surface. In this case, unusually high carbon isotope ratios of dentine from some sites within the two areas provide the first direct evidence of CH₄ production in coastal floodplains of western North America during the

Late Cretaceous. Such production of CH₄ likely played an important role as a feedback that helped maintain “hothouse” climate conditions during this time.

Since CH₄ production has a pronounced impact on carbon isotope ratios of gases being emitted from the soil surface, it is possible to trace the movement of these gases into the biotic reservoir. In particular, the existence of hadrosaurid tooth enamel with high carbon isotope ratios suggests that these gases were incorporated into low-level forest vegetation before being eaten by the animals. In order for such “recycling” of carbon to occur, it is necessary for there to be a closed canopy near the surface, meaning that the forest understory is isolated from the open atmosphere due to dense vegetation cover. Thus, results from this study provide the first direct evidence for dense closed canopy forests in southern Utah during the Late Cretaceous.

1. Introduction

During the late Mesozoic, the convergence between the North American Plate and the Farallon Plate resulted in the Sevier Orogeny, an event that produced folding and thin-skinned thrust faulting and associated north-south trending mountain ranges throughout North America (Pang and Nummedal, 1995; Horton et al., 2004). At the same time, high global sea levels resulted in the flooding of central North America and the formation of the Cretaceous Western Interior Seaway (KWIS), which split North America into two land masses (Fig. 1). This produced relatively narrow north-south trending belts of eroding mountains, as well as areas of both fluvial-floodplain and estuarian-coastal deposition in what is now a fully terrestrial environment (Fig. 1).

In the case of southern Utah, sedimentological and floral analyses of the Campanian Kaiparowits Formation indicate that the area was an alluvial plain in a sub-humid climate that experienced seasonal variation in precipitation resulting in times of abundant precipitation but also times of aridity (Roberts, 2007), comparable to the modern-day Gulf Coast (Miller et al., 2013; Roberts et al., 2013.). Within the alluvial plain, there were meandering and anastomosing channels, crevasse splays, floodplains, oxbow lakes, swamps and tidally influenced channels (Roberts, 2007). In particular, the floodplain environments hosted an abundance of wetlands, ponds and lakes (Roberts et al., 2013).

The diverse fauna living in these environments include fish, amphibians, reptiles, mammals, and dinosaurs. The majority of fossils recovered from formations of this age are ornithischian herbivores (hadrosaurids and ceratopsians), with hadrosaurids sometimes accounting for half. Other vertebrate taxa represented in the assemblage of the

Kaiparowits consist of a variety of fish, amphibians, squamata, turtles, crocodiles, mammals, and a wide variety of dinosaurs.

The flora was dominated by angiosperms, based on species and morphotype abundance collected from an extensively sampled site in the Kaiparowits, the majority of which are dicot morphotypes. There are also some gymnosperms, such as conifers and cycads, as well as some types of ferns (Miller et al., 2013).

In addition to a variety of unique flora and fauna, southern Utah during the Late Cretaceous had very different climatic conditions than at present. In general, “hothouse” conditions existed globally, as evidenced by the lack of polar ice caps. Locally, there were higher temperatures and more precipitation (DeConto et al., 2000; Fricke et al., 2010 and references therein). For example, climate modeling and isotope analyses by Fricke et al. (2010) reveal that the Western Interior experienced a strong monsoon during the Campanian, which is supported by the global climate model simulations of Sewall and Fricke (2013). In addition, temperatures during the Campanian were approximately 10°C higher than present day (DeConto et al., 2000). The poles, specifically, were significantly warmer, as evidenced by the fossil assemblage of flora and fauna found in polar formations (Huber, 1998), giving a lower latitudinal temperature gradient (Wolfe and Upchurch, 1987). High levels of atmospheric CO₂ are thought to have been the primary causes of hothouse climates in the past, including the Late Cretaceous (DeConto et al., 2000; Fletcher et al., 2008), although recent climate model results suggest that high CH₄ concentrations also contributed to additional warming (Beerling et al., 2009; Beerling et al., 2011). The source of this CH₄ is not known for certain, but it has been

hypothesized that terrestrial wetlands played a major role in its production (Beerling et al., 2009; Beerling et al., 2011).

Despite what is known about the fluvial-coastal environments adjacent to the KWIS in southern Utah and the plants and animals occupying these environments, several questions remain unanswered. For example, do the large populations of herbivorous dinosaurs that share the landscape partition dietary resources? If so, how? Such partitioning is observed for modern mammals and has been described for dinosaurs from the Cretaceous in North Dakota (Fricke and Pearson, 2008). More generally, are there any specific characteristics of Late Cretaceous forests in this area that enabled them to support such a large number and variety of herbivorous animals? Lastly, is there any direct evidence for CH₄ production in floodplain and/or coastal wetlands that could have influenced Late Cretaceous climate? In an effort to answer all of these questions, a stable isotope study of vertebrate fossil remains was undertaken, the results of which are described herein.



Figure 1: Late Cretaceous North America. Locations of contemporaneous Late Cretaceous WIB formations containing hadrosaur fossils. (A) Dinosaur Park Formation, Alberta, Canada; (B) Two Medicine Formation, Montana; (C) Judith River Formation, Montana; (D) Hell Creek Formation, Montana, North Dakota and South Dakota; (E) Kaiparowits Formation, Utah; (F) Fruitland and Kirtland Formations, New Mexico; (G) Aguja Formation, Texas. Adapted from Ron Blakey.

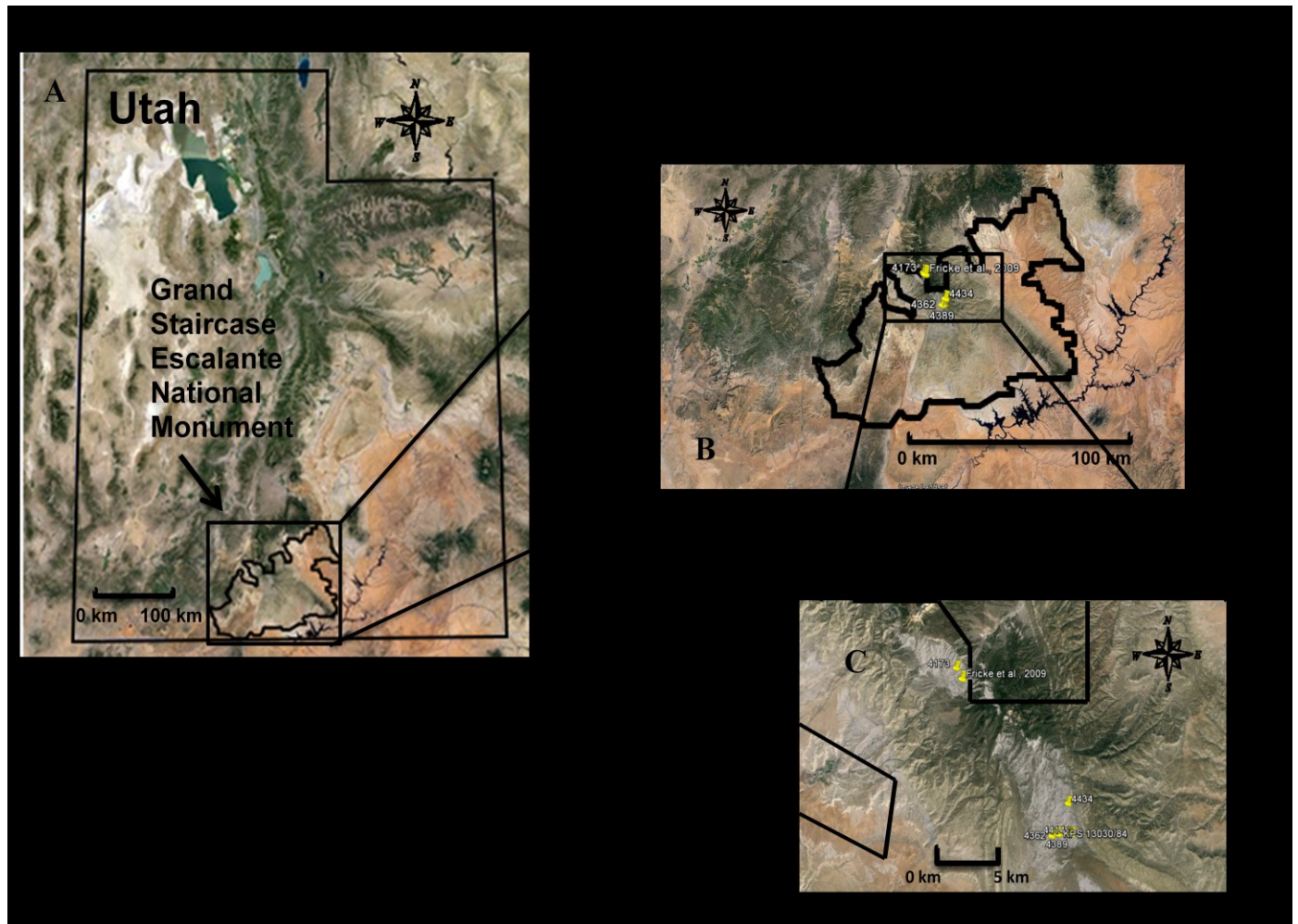


Figure 2: Location of sample localities. (A) Location of Grand Staircase Escalante National Monument (GSENM) within Utah, U.S.A. (B-C) Location of sample localities within Grand Staircase Escalante National Monument. Numbers correspond to Denver Museum of Nature and Science (DMNS) locality numbers. The sample localities have been grouped into three general locations: the Blues, VCKP1 and VCKP2. The northern-most location is the Blues, and it consists of site 4173 and the site from Fricke et al., 2009. VCKP1 consists of site 4434, and VCKP2, the southern-most location, consists of sites 4389, 4414, 4362, 4418 and 13030/84.

2. Background

2.1 Stable isotope ratios and past environments

Isotopes are atoms of the same element that contain the same number of protons in the nucleus, but a different number of neutrons; this gives different isotopes different masses. Stable isotopes with larger masses form stronger chemical bonds and move at slower velocities (due to their lower vibrational frequency), which cause a differentiation, or fractionation, of isotopes during physical and chemical processes that allows the movement of isotopes to be traced through different chemical reservoirs. This fractionation of isotopes provides different materials and environments with distinct isotope signals. These isotope signals are the ratio of the heavier isotope to the lighter isotope of the sampled material, compared to the heavy to light isotope ratio of a standard. Isotope ratios are reported using the “ δ ” notation with δ referring to $(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} * 1000\text{‰}$, where R is the ratio of the heavy isotope to the light isotope. The standard for carbon is PDB and the standard for oxygen is SMOW. In general, isotope ratios are useful tools for the study of paleoenvironments because of the ubiquitous occurrence of carbon and oxygen isotopes in a variety of different chemical reservoirs such as the biosphere and hydrosphere.

2.1.1 Isotopic variations in plants and water over a landscape

Carbon and oxygen isotope ratios of plants and water vary across landscapes. More specifically, C_3 plants, which predominated during the Mesozoic, isotopically discriminate between carbon isotopes during photosynthesis, preferentially incorporating ^{12}C so that the average carbon isotope ratio (i.e. $\delta^{13}\text{C}$) is -26‰ (Fricke et al., 2008). $\delta^{13}\text{C}$

of these plants are also influenced by environmental factors such as temperature, availability of water and nutrients, light intensity and salinity. When these factors are unfavorable to plant survival and plants become stressed, leaf stomata, which allow CO₂ into the cell, are often closed, preventing most CO₂ from entering the leaf cell. This affects the carbon isotope ratio of the plant by preventing the plant from discriminating against ¹³C. Spatial variation in the degree to which plants in different areas open or close their stomata creates a variation of δ¹³C across landscapes (Kohn and Cerling, 2002; Fricke and Pearson, 2008; Fricke et al., 2009). In addition, oxygen isotope ratios (i.e. δ¹⁸O) may also vary across landscapes due to variable environmental conditions, such as temperature and aridity, as well as the rainout “history” of the air masses that bring precipitation to a region (Fricke and Pearson, 2008; Fricke et al., 2008; Fricke et al., 2009). As an air mass moves away from the coast or over mountains, preferential rainout of the ¹⁸O occurs, resulting in a decrease of oxygen isotope ratios farther inland. This precipitation will also interact with existing surface and ground water and undergo evaporation, producing an even greater variability across landscapes (Fricke et al., 2008). The variability of both carbon and oxygen isotope ratios within a landscape results in the formation of distinct isotope domains within a region, each with its own characteristic carbon and oxygen isotope ratios (Fricke and Pearson, 2008; Fricke et al., 2009). The unique isotope ratios of each domain are then recorded by the herbivores that reside there and ingest the plants and water within it.

2.1.2 Vertebrate tooth enamel as a record of plant and water isotope ratios

Isotope ratios of plants and water ingested by dinosaurs are recorded in the

carbonate in bioapatite, $[\text{Ca}_5(\text{PO}_4, \text{CO}_3)_3(\text{OH}, \text{CO}_3)]$, a component of tooth enamel. The carbon in the carbonate of the bioapatite is sourced from the carbon of ingested plant material, and the oxygen comes from the surface water consumed by the organism as well as from atmospheric oxygen. Since atmospheric oxygen isotope ratios have generally remained constant at $\sim 23\text{‰}$, it can be inferred that any variation in oxygen isotope ratio is the result of variations in surface water isotope ratios. Thus, the carbon and oxygen isotopes of dinosaur tooth enamel can be utilized to determine their preferred isotope domain and microhabitat (Fricke and Pearson, 2008; Fricke et al., 2009).

Through the comparison of relative differences of enamel isotope ratios, insight into the ecology, environment and distribution of dinosaurs can be gained. For example, this approach has been used to: 1) understand and compare the microhabitats of hadrosaurids and paleoenvironments in the Judith River and Two Medicine Formations (Fricke et al., 2008); 2) determine if there was any niche partitioning among hadrosaurids and ceratopsians in the Hell Creek Formation of North Dakota (Fricke and Pearson, 2008); and 3) provide insight into hadrosaurid migratory behavior during the Late Cretaceous in North America (Fricke et al., 2009).

2.1.3 Isotope ratios of tooth dentine as a record of soil processes

Although variations in isotope ratios of tooth enamel are generally due to differences in herbivore behavior and ecology, variations in isotope ratios of tooth dentine are generally due to diagenetic processes. Unlike tooth enamel, tooth dentine is more porous and more prone to isotopic resetting during diagenesis. Diagenesis is defined as the post-mortem chemical alteration of bioapatite. It occurs through two

processes: interaction with fluids causing isotopic exchange between bioapatite and the fluids and the precipitation of secondary carbonate or apatite from the fluids (Fricke et al., 2008). In fact, past studies (Fricke and Pearson, 2008; Fricke et al., 2008; Fricke et al., 2009) of enamel and dentine from dinosaur teeth of the Late Cretaceous suggest that dentine reflects diagenetic (i.e. burial) conditions rather than primary ecological information (a similar argument is made in this study). As a result, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of dentine can be used to study burial environments and the biogeochemical processes taking place within them.

One such process is the oxidation of organic matter, which occurs in well-drained surface settings with open connections to the atmosphere:



The source of this organic matter is leaf litter shed from trees. Carbon isotope fractionation does not take place during this process, so the $\delta^{13}\text{C}$ of the CO_2 produced is equal to the $\delta^{13}\text{C}$ of the C_3 plant matter, $\sim -30\text{‰}$ to -23‰ (Fig. 8). This CO_2 can either diffuse through soils into the atmosphere, or it can dissolve into the groundwater where it can then be incorporated into authigenic carbonate, including secondary carbonate that precipitates in the pore spaces of tooth dentine. This carbonate typically has $\delta^{13}\text{C}$ values approximately 14‰ higher than the CO_2 itself due to the temperature-dependent and kinetic isotope fractionation that takes place as it forms (Koch, 1998).

Another process that can take place in anoxic, poorly-drained, near-surface freshwater environments is bacterial methanogenesis (Whiticar, 1999):



Fractionation of carbon isotopes by bacteria called methanogens gives the CH₄ and CO₂ produced during methanogenesis distinctive $\delta^{13}\text{C}$ values (Whiticar, 1999). This process preferentially incorporates ¹²C into the CH₄, and produces CH₄ with very low $\delta^{13}\text{C}$ of -110‰ to -50‰ (Whiticar, 1999). Conversely, the CO₂ has very high $\delta^{13}\text{C}$ of up to +10‰ to +15‰ (Irwin et al., 1977; Bowen and Bloch, 2002).

As in the case of CO₂ forming via oxidation, CO₂ forming via methanogenesis can either diffuse through soils into the atmosphere or dissolve into groundwater where it can be incorporated into authigenic carbonate including carbonate forming in the pore space of the dentine. The key difference is that this carbonate will have $\delta^{13}\text{C}$ values that are significantly higher than $\delta^{13}\text{C}$ values associated with the oxidation of organic matter (Bowen and Bloch, 2002; Jahren et al., 2004).

3. Methods

Hadrosaurid teeth, whole and fragmentary, were collected from 10 different microsite localities within the Kaiparowits Formation located in south-central Utah in Grand Staircase Escalante National Monument (GSENM) (Fig. 2). Argon-Argon dating of bentonite layers provides a high-resolution age of the Kaiparowits Formation ranging from 76.6 – 74.5 Ma (Roberts et al., 2005; Roberts et al., 2013).

The microsite localities are grouped into three general locations: the Blues, VCKP1 and VCKP2 (Fig. 2). It was not possible to make direct stratigraphic correlations between these sites, but the Blues sites are ~ 280 m above the base of the formation and the VCKP1 and VCKP2 sites are ~150 m above the base of the formation (Roberts et al., 2007).

The teeth were analyzed using methods very similar to those employed by Fricke and Pearson (2008), Fricke et al. (2008), and Fricke et al. (2009). Samples, weighing approximately one milligram, of the tooth enamel and dentine were extracted using a diamond-tipped dremel drill. These samples were then soaked in 0.1 M acetic acid for 24 hours, rinsed three times and then dried for 24 hours. This removed any secondary authigenic carbonate that is more susceptible to chemical changes, as well as any contaminated carbonate (Kohn and Cerling, 2002). $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were obtained using an automated carbonate preparation device (KIEL-III) and a Finnegan MAT 252 isotope ratio mass spectrometer at the University of Arizona (Fricke and Pearson, 2008). There, the powdered samples of enamel and dentine were reacted with phosphoric acid in a vacuum at high temperatures alongside silver foil. International reference standards of NBS-19 and NBS-18 were used, as well as carbonate standards based on samples

available in the laboratory (Fricke et al., 2009). The analytical precision for both ratios is $\pm 0.1\%$.

Resulting stable isotope data were then statistically analyzed and graphed using Microsoft Excel. F-tests were used to determine if the variances were equal or unequal and then corresponding t-tests (assuming equal or unequal variances) to compare the means were applied (Table 2). In addition, R, a statistics program, was used to test for bimodality.

4. Results

Statistical analyses of the data reveal that there are significant differences in $\delta^{13}\text{C}$ between hadrosaurid enamel and dentine and between the three locations: the Blues, VCKP1 and VCKP2. (The raw data are found in Table 1 and the results of statistical tests of the data are found in Table 2.) The hadrosaurid dentine generally has higher and more variable $\delta^{13}\text{C}$ compared to enamel of the same site, and the $\delta^{13}\text{C}$ of enamel is significantly different among the sites. Of the three sites, VCKP2 has the highest $\delta^{13}\text{C}$ values, as well as the highest variability. In contrast, the Blues has the lowest $\delta^{13}\text{C}$ values.

5. Discussion

5.1. Diagenesis and preservation of primary ecological information in hadrosaurid tooth enamel

In order for tooth enamel to be useful as a paleoecological tool, it is necessary to demonstrate that primary isotopic information is preserved in hadrosaurid tooth enamel. This has been done previously for the Blues (Fricke et al., 2009), and the same approaches are used in this study. One such approach involves a comparison of oxygen and carbon isotope data between enamel and dentine of the same fossil element. In this case, $\delta^{13}\text{C}$ values and variance are significantly larger for dentine compared to enamel for each locality (Fig. 3 and 4, and Table 2). The elevated $\delta^{13}\text{C}$ values of the dentine are assumed to be moving toward a diagenetic end member with much higher $\delta^{13}\text{C}$ values. Isotope ratios of the enamel, however, have not been altered to the same degree (i.e. there is no isotopic trend towards the diagenetic end member) and are thus assumed to preserve the initial isotope signals.

A second approach involves a comparison of oxygen and carbon isotope data between taxa from the same location. Offsets are expected, as different taxa with different physiologies utilize carbon and oxygen in different ways. Comparisons between hadrosaurid enamel and gar ganoine have previously been made for the data collected from the Blues (Fricke et al., 2009), and distinct isotopic offsets have been observed. These offsets in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ most likely reflect a difference in physiology or ecology between the hadrosaurids and the gar, and thus provide additional evidence that diagenetic alteration has not completely obscured the original isotopic signals in the Kaiparowits.

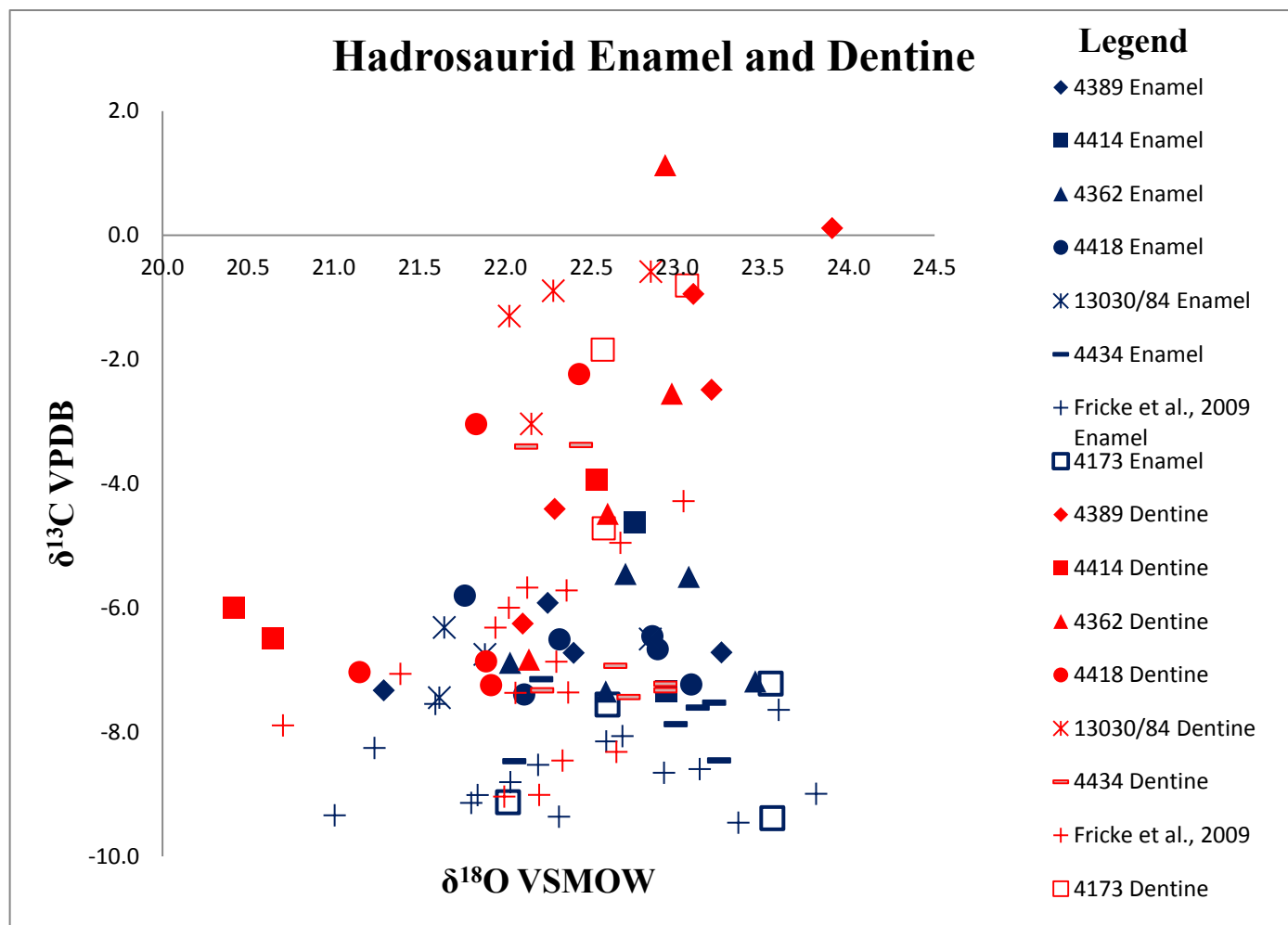


Figure 3: Hadrosaurid enamel and dentine. Comparison of enamel (blue) and dentine (red) from the same hadrosaurid tooth for all three localities. Offset between the dentine and the enamel and higher dentine values indicate that dentine has been diagenetically altered to a higher degree than the enamel. This suggests that primary isotope signals have been preserved.

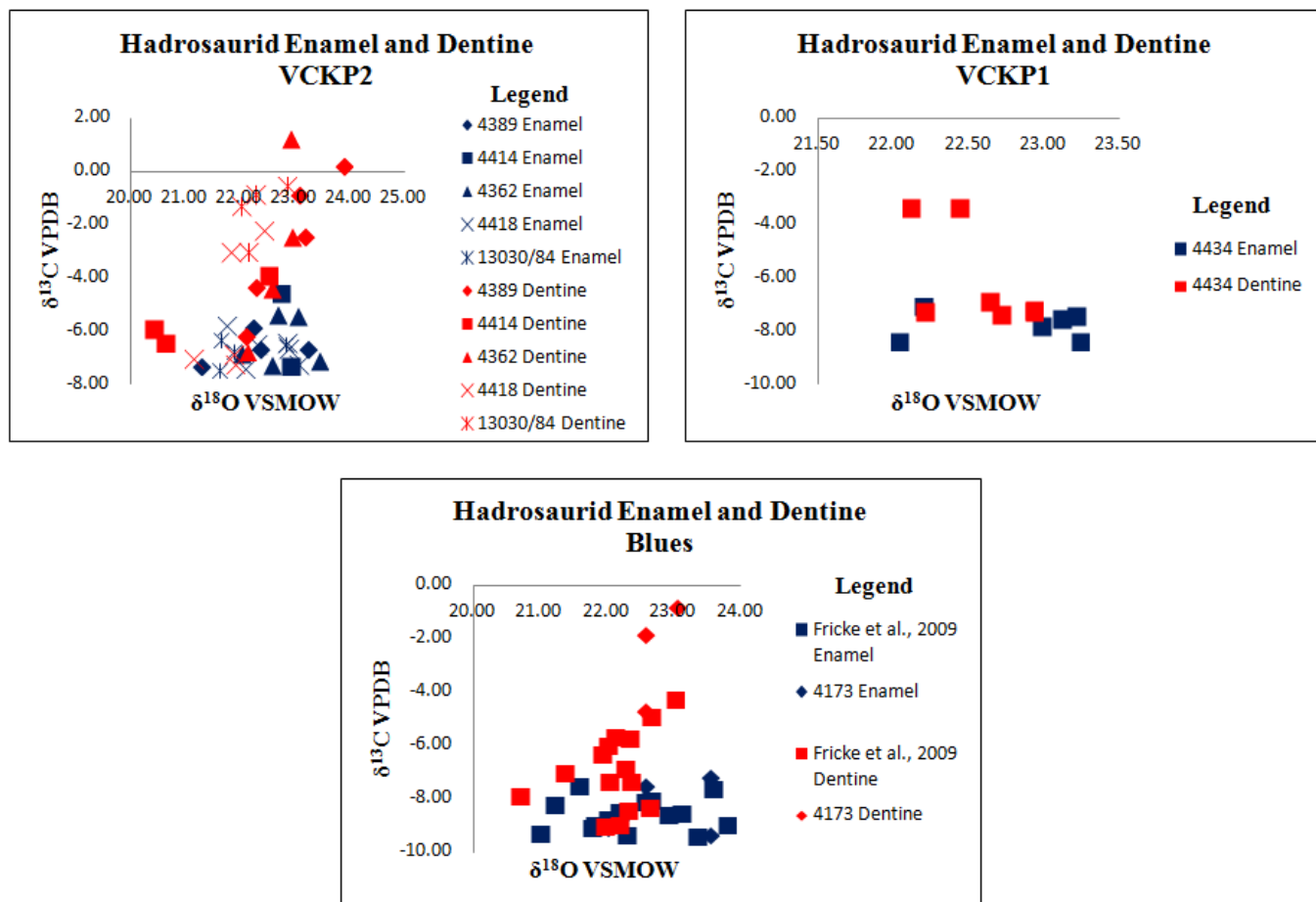


Figure 4: Hadrosaurid enamel and dentine by locality. Comparison of enamel (blue) and dentine (red) from the same hadrosaurid tooth for all three localities individually. Offset between dentine and enamel suggests a higher degree of diagenetic alteration of the enamel from all three sites.

5.2 Enamel isotope ratios and hadrosaurid niche partitioning

There is a significant offset in $\delta^{13}\text{C}$ of tooth enamel between the different sampling areas (i.e., the Blues, VCKP1 and VCKP2; Table 2; Fig. 5). There are several possible explanations for this offset. One is that the three localities represent different microenvironments that each provided its own unique type of plant community (i.e. diet) consumed by hadrosaurids. Since different plant types can have different $\delta^{13}\text{C}$ (e.g. angiosperms vs. gymnosperms), such a difference in plant communities could have produced the observed isotopic offset between the three localities. The second is that a distinct difference in environmental conditions existed over the landscape such that $\delta^{13}\text{C}$ of plants were higher in areas where there was greater environmental stress on plants. Hadrosaurids may have consumed plants in these areas as well as in areas without high environmental stress, resulting in the observed $\delta^{13}\text{C}$ offset. Lastly, it is possible that the recycling of CO_2 in the understory of a closed forest canopy in one part of the landscape led to a modification of plant $\delta^{13}\text{C}$ values in the understory. Exclusive hadrosaurid consumption of plants from either the forest understory or from other non-closed canopy areas may have produced the isotopic offsets among hadrosaurid populations observed in the tooth enamel.

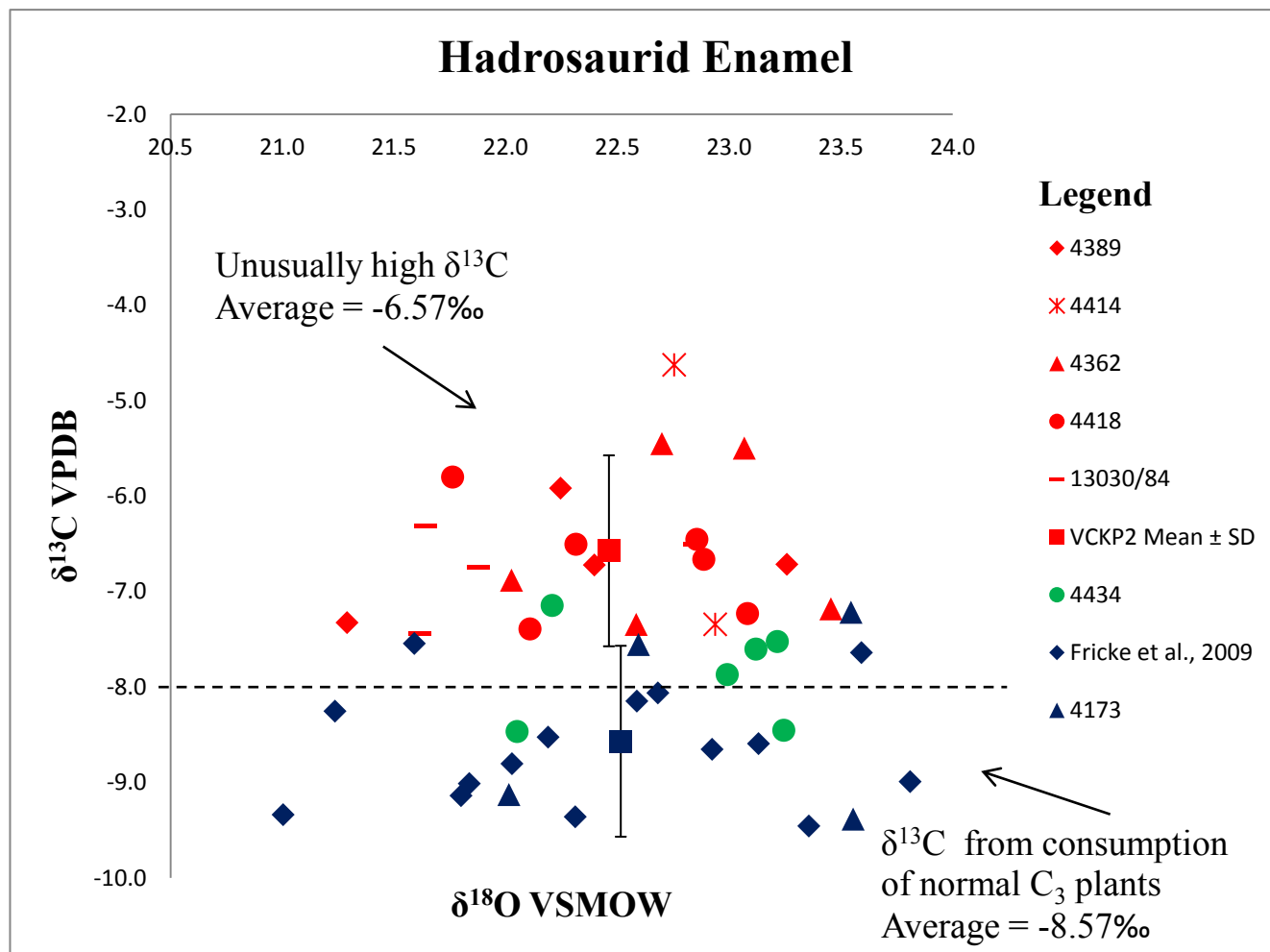


Figure 5: Hadrosaurid enamel. Comparison of hadrosaurid tooth enamel from the three Kaiparowits localities: the Blues (blue), VCKP1 (green) and VCKP2 (red). This plot shows a significant statistical isotopic offset between the $\delta^{13}\text{C}$ of the three locations. This offset can be explained by a difference in plant type between the locations, difference in environmental and climatic stressors, or a modification of $\delta^{13}\text{C}$ by the canopy effect. $\delta^{13}\text{C}$ values below the dotted line can be explained by consumption of normal C_3 plants. Anything above the line is unusually heavy and can be explained by consumption of plants from the forest understory that have incorporated methanogenically derived CO_2 with unusually high $\delta^{13}\text{C}$.

There are generally two types of sedimentological facies associations that host fossil microsites in the Kaiparowits: pond and fluvial (Roberts et al., 2013). Flora generally varied greatly across Campanian landscapes, so it is likely that these two different types of microenvironments hosted different types of plants. Floodplains and similar environments within this region were primarily dominated by angiosperms, whereas river channels and other similar environments were dominated by conifers (Upchurch and Wolfe, 1993; Wing and Boucher, 1998; Wing et al., 2012). These two plant types fractionate carbon to different degrees, resulting in a difference in $\delta^{13}\text{C}$ of the two plant types. Angiosperms have $\delta^{13}\text{C}$ values that are approximately 2‰ to 3‰ lower than their gymnosperm counterparts (Heaton, 1999; Van de Water et al., 2002; Schouten et al., 2007), but the difference between the two can be as low as 1‰ (Diefendorf et al., 2009). Thus, teeth from hadrosaurids that consumed a primarily angiosperm-based diet could potentially have significantly lower $\delta^{13}\text{C}$ values. This could account for why the Blues site, which records more of a floodplain environment, has the lowest $\delta^{13}\text{C}$ values of the three localities in the Kaiparowits, and why, by contrast, VCKP2 has the highest (Fig. 6).

The influence of other environmental factors could also explain the difference in $\delta^{13}\text{C}$ between the three localities. As mentioned previously, when plants are stressed, they tend to keep their stomata closed, which results in a decrease of carbon fractionation during photosynthetic processes and therefore an increase in $\delta^{13}\text{C}$ of stressed plants. Thus, the higher $\delta^{13}\text{C}$ of VCKP2 can be explained by a greater influence of environmental stressors in that locality. In addition, other environmental factors, such as the canopy effect, can result in changes in the $\delta^{13}\text{C}$ of plants.

The “recycling” of carbon can lead to a modification in $\delta^{13}\text{C}$ of plants beneath a dense closed canopy (van der Merwe and Medina, 1991; Drucker et al., 2008). Generally, the modification in $\delta^{13}\text{C}$ is considered to be the result two main factors, including 1) the recycling of CO_2 from organic material degradation on the forest floor (van der Merwe and Medina, 1991; Drucker et al., 2008) due to poor ventilation in the understory that does not allow mixing of this air with that of the open atmosphere; and 2) the resulting change in photosynthesis and stomata opening and closing due to limited amounts of CO_2 , light, and possibly water in the forest understory (Drucker et al., 2008). A larger canopy effect in one area compared to another could be the reason for a relative difference in $\delta^{13}\text{C}$ of plants. This difference then gets recorded in the tooth enamel of the hadrosaurids occupying the different areas. Informal hypotheses about the forest structure have been made by paleobotanists and paleontologists familiar with the region, proposing that there must have been dense closed canopy forests in parts of the landscape in order to provide enough vegetation to sustain large populations of megaherbivores (Miller, 2014).

Of these three hypotheses for the $\delta^{13}\text{C}$ offset, the most parsimonious explanation would be the modification of $\delta^{13}\text{C}$ by the canopy effect. When considering the first hypothesis, in order for differing plant communities to cause the 2‰ change in average $\delta^{13}\text{C}$ values observed between the two sites, the Blues and VCKP2, the hadrosaurid sub-populations inhabiting these two areas would need to have been eating *only* angiosperms or gymnosperms respectively. It has been suggested that hadrosaurids were generalist herbivores, so it is unlikely that populations of hadrosaurids differentiated between plant types and exclusively restricted their diets to one specific plant type (Wing and Tiffney, 1987; Fastovsky and Smith, 2004). In addition, the second hypothesis, that some

hadrosaurid populations consumed only stressed plants and the other consumed only non-stressed plants, is also not likely. Stressed environments generally do not contain a diversity of fossils and may contain only one taxa (Eberth et al., 2007). Fossil localities within the Kaiparowits are generally quite diverse in their flora and fauna (Miller et al., 2013; Sampson et al., 2013), and, therefore, are less likely to represent stressed environments. Thus, the modification of $\delta^{13}\text{C}$ by the canopy effect is the most likely explanation for the observed $\delta^{13}\text{C}$ offset.

Regardless of the exact explanation for the differences in $\delta^{13}\text{C}$ of tooth enamel between the sites, its existence alone is evidence for ecological niche partitioning among hadrosaurid populations occupying the Kaiparowits landscape – meaning that different populations of hadrosaurid sub-families, lambeosaurine and hadrosaurine, were occupying each microenvironment exclusively. Such behavior has previously been proposed for Late Cretaceous hadrosaurids. For example, a study by Carrano et al. (1999) used modern horned ungulates as analogues of North American hadrosaurid sub-families to suggest that hadrosaurines would prefer floodplain environments and that lambeosaurines would prefer channel environments. It is likely that hadrosaurids of the Kaiparowits were partitioning resources in this manner. A similar partitioning of resources is also observed for hadrosaurids and ceratopsians from the Hell Creek Formation, as described by Fricke and Pearson (2008). This partitioning of resources makes sense within the context of the limited range that North American hadrosaurids were thought to have inhabited, given the hypothesis of hadrosaurid provincialism that arose from analysis of the latitudinal distribution of flora and fauna and stable isotope studies of tooth enamel.

Analyses of the fossil assemblages throughout North America, particularly by Lehman (1997), reveal latitudinal faunal zones, with distinct north and south end members, and a gradient or zone of faunal mixing between them (Lehman, 1997; Lehman, 2001). In general, these north-south faunal zones have the same broad faunal structure and collection of organisms on the family level. It is on the genus and species levels that the fauna differ (Gates et al., 2010). Thus, this significant regionally restricted distribution of fauna provides strong evidence against large-scale migration, which is corroborated by stable isotope analyses that indicate that hadrosaurids did not undertake extensive east-west or north-south migrations (Fricke et al., 2009) during the Late Cretaceous. Given this non-migratory behavior, the evidence of hadrosaurid niche partitioning in this study provides insight into how these large populations of hadrosaurids were maintained, considering the limited resources within the narrow range that they inhabited. In addition, the presence of a closed canopy forest within the Kaiparowits would suggest that there were resources sufficient enough to sustain such large populations of hadrosaurids within this narrow range.

In summary, isotopic offsets between the Blues and VCKP2 indicate that different populations of hadrosaurids inhabited different microenvironments characterized by distinct $\delta^{13}\text{C}$ within the alluvial plain of the Kaiparowits Formation. The differences in $\delta^{13}\text{C}$ could be caused by a difference in plant type, presence of environmental stressors, and other environmental influences including the canopy effect.

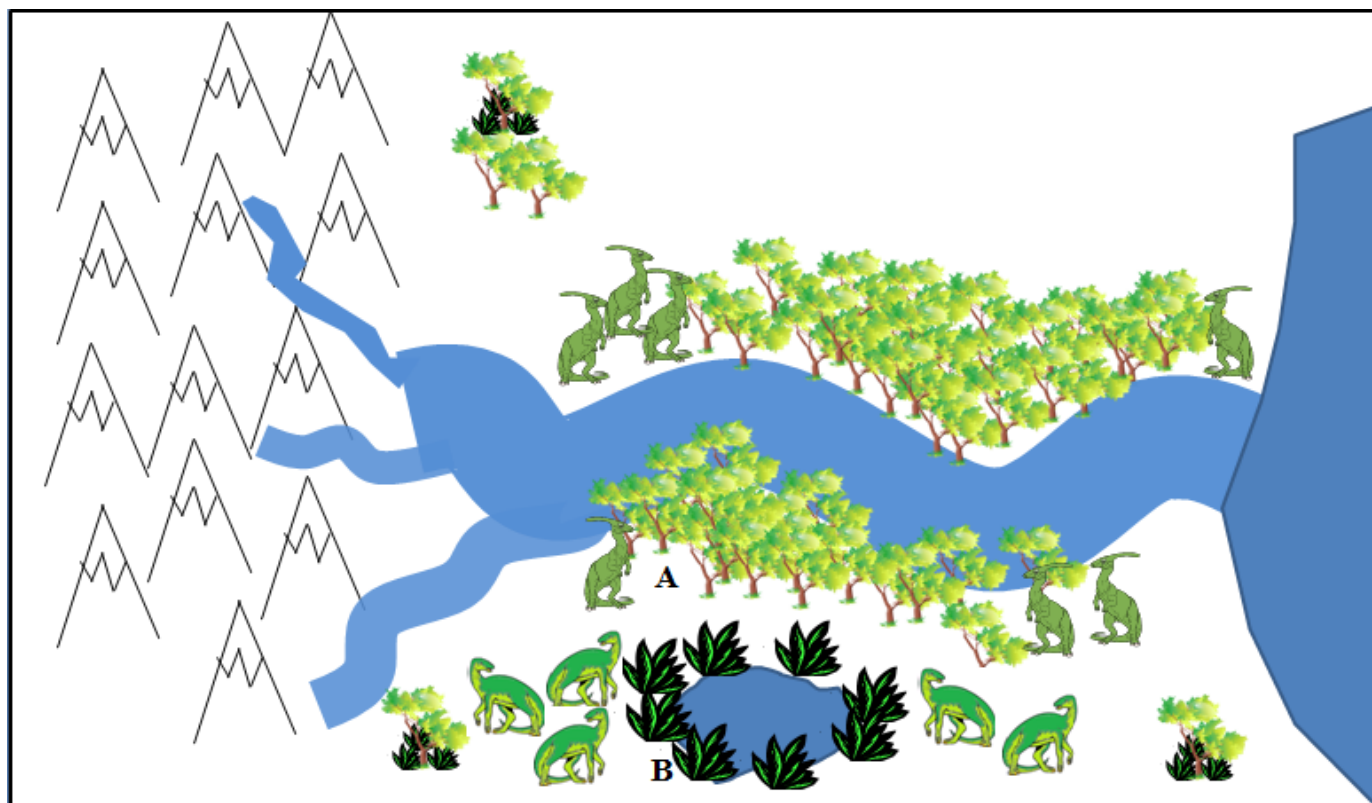


Figure 6: Interpretation of paleoenvironments. Interpretation of paleoenvironments of the Kaiparowits Formation. (A) indicates a possible microenvironment habitat for hadrosaurids from the VCKP2. Higher $\delta^{13}\text{C}$ could be the result of a flora dominated by gymnosperms, a higher presence of environmental stressors or a modification of $\delta^{13}\text{C}$ by the canopy effect. This type of microenvironment was preferred by lambeosaurines. (B) indicates a potential microenvironment for the Blues, with lower $\delta^{13}\text{C}$ due to the dominance of angiosperms, an absence of environmental stressors and a lesser degree of modification of $\delta^{13}\text{C}$ by the canopy effect. This type of microenvironment was preferred by hadrosaurines.

5.3 Landscape variability in redox conditions and methane production

Given the more porous nature and smaller apatite crystal size of tooth dentine, it is more susceptible to diagenetic alteration than enamel, and thus stable isotope data from it does not provide useful paleoecological information. Such data from dentine can, however, provide insight into diagenetic processes, redox and drainage conditions of soils. In particular, $\delta^{13}\text{C}$ of dentine can be used to identify soil processes that were responsible for the production of CO_2 incorporated into diagenetic fluids, and then into authigenic carbonate within the dentine. Since oxidation of organic matter and methanogenic breakdown of organic matter produce CO_2 with markedly different $\delta^{13}\text{C}$ values (-30‰ to -23‰ and +10‰ to +15‰ respectively; see section 2), $\delta^{13}\text{C}$ of dentine should be useful in recognizing one process or the other taking place in the geologic past.

Diagenetic alteration has not affected the dentine of the hadrosaurid teeth in the same way everywhere (Fig. 7). $\delta^{13}\text{C}$ of the dentine in the VCKP2 locality are statistically significantly higher than those of the Blues. This suggests that there was a difference in the soil/groundwater diagenetic processes and redox conditions. More specifically, the comparatively low $\delta^{13}\text{C}$ of the Blues dentine indicates that diagenetic CO_2 was derived from the oxidation of organic matter. This oxidation process would have occurred in a well-drained surface environment (Fig. 8). In contrast, the elevated $\delta^{13}\text{C}$ of the VCKP2 locality are indicative of methanogenically derived CO_2 in groundwater. Thus, this provides evidence that the soils of VCKP2 were anoxic, reducing environments that favored the processes of methanogenesis. In turn, this suggests that the microenvironment represented by this location was low-lying and waterlogged, perhaps reflecting a swamp or other year-round wetland environment (Fig. 9).

5.4 Implications of evidence for methane production along the coast of the KWIS

5.4.1 Impact of methane production on Late Cretaceous climate

Global climate simulation models (Beerling et al., 2011) suggest that wetland environments were the source of the elevated concentration of CH₄ in the atmosphere and that, since CH₄ is a strong greenhouse gas, this CH₄ may have been responsible for increased radiative forcing and increased global temperatures during the Late Cretaceous (Beerling et al., 2011). In particular, the model suggests that CH₄ production that occurred specifically in wetland soils in the Northern Hemisphere during this time was responsible for global mean concentrations of CH₄ nearly double that of today (Beerling et al., 2011). However, this model is limited, as it relies on the simulation of terrestrial, climatic, and atmospheric processes and lacks geochemical and biological proxies to provide evidence of this CH₄ concentration and production in soils (Beerling et al., 2011). The results of this study, however, provide the first direct evidence for Late Cretaceous diagenetic CH₄ production in wetland environments. The water-logged reducing environments represented by the VCKP2 locality would have been emitting CH₄ into the Late Cretaceous atmosphere during this hothouse time period (Fig. 9). This study therefore provides important support for the hypothesis that elevated atmospheric CH₄ concentrations were an important climate forcing mechanism at this time. Furthermore, this study suggests that dinosaur tooth dentine can serve as a new proxy for recognizing and mapping paleo-methane production in soils. This proxy can be used in conjunction with climate modeling to understand climate feedbacks in hothouse worlds of the past.

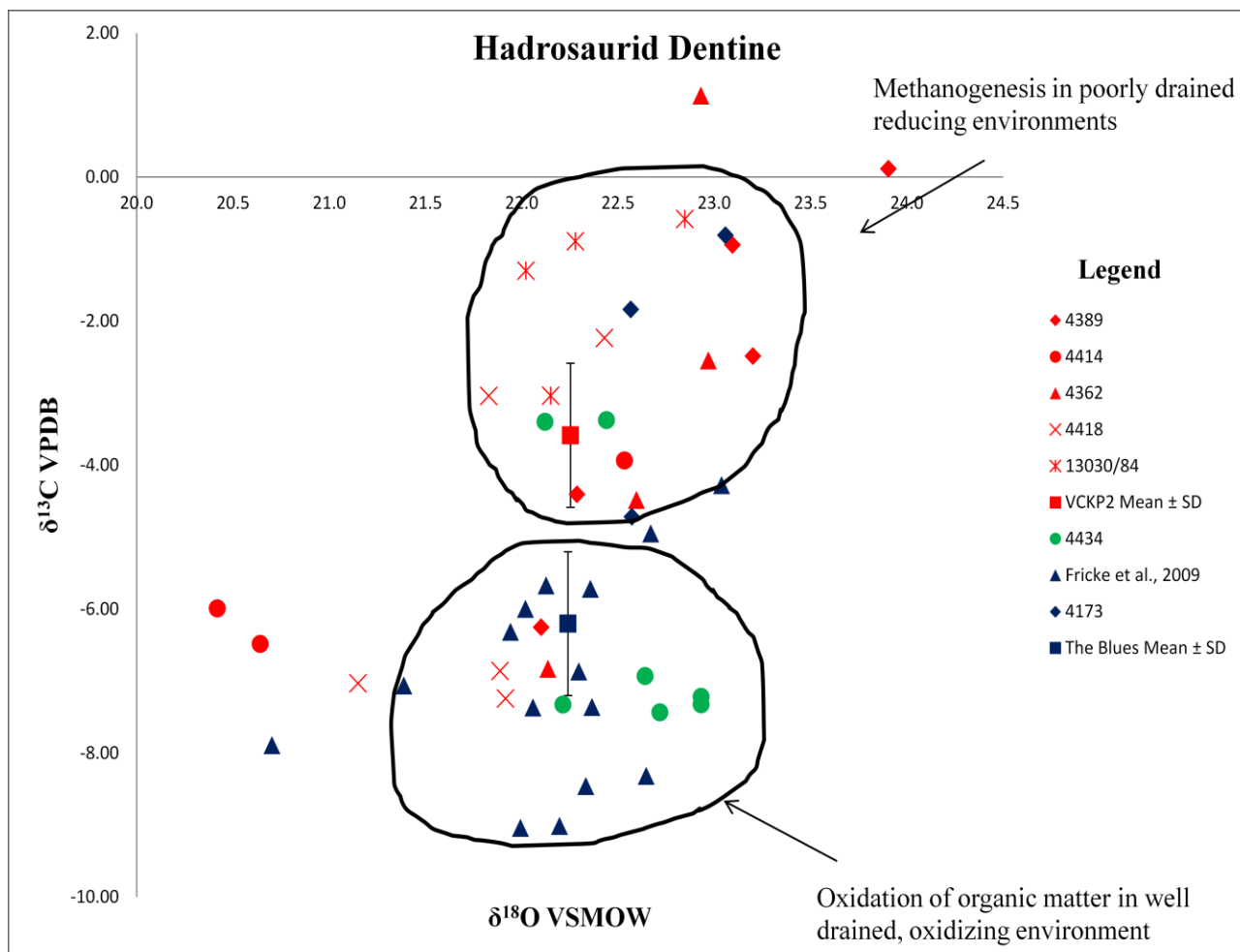


Figure 7: Hadrosaurid dentine. Comparison of hadrosaurid tooth dentine from the three Kaiparowits localities: the Blues (blue), VCKP1 (green), and VCKP2 (red). Higher $\delta^{13}\text{C}$ of dentine from teeth at VCKP2 provide evidence of methanogenesis in a poorly drained reducing environment. Lower $\delta^{13}\text{C}$ of dentine from teeth at the Blues and VCKP1 are consistent with less or limited methanogenesis in a well drained oxidizing environment.

5.4.2 Methane production and forest structure of the Kaiparowits landscape

The incorporation of CO₂ derived from methanogenesis into understory vegetation may be the primary reason that hadrosaurid tooth enamel from the VCKP2 locality has higher $\delta^{13}\text{C}$ than the Blues. It is possible that methanogenically derived CO₂ produced in soils was emitted into the atmosphere, where it became incorporated into terrestrial plants via the canopy effect. This would result in the enhanced cycling of ¹³C through the forest understory environment, enriching the forest understory plants with ¹³C and, thus, giving them higher $\delta^{13}\text{C}$ than plants living in more open floodplain environments. Herbivores occupying the understory of closed canopy forests consuming these plants would, in turn, have higher $\delta^{13}\text{C}$ of their tooth enamel. In other words, $\delta^{13}\text{C}$ of several trophic levels (i.e. from photosynthesizers to herbivores) may have been impacted by CH₄ production in water-logged soils (Fig. 9). If this interpretation is correct, it represents the first direct geochemical evidence of a dense closed canopy environment within the Kaiparowits Late Cretaceous landscape.

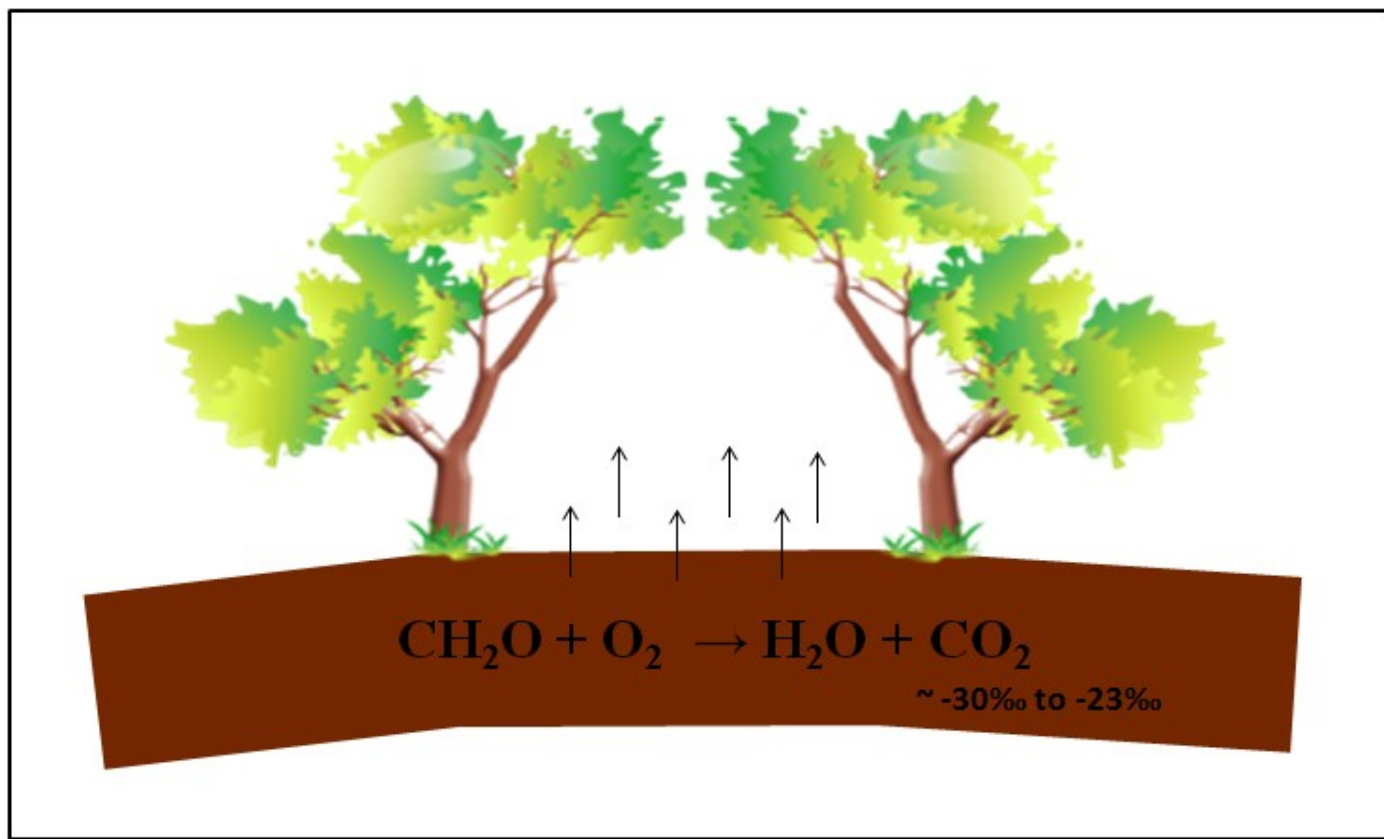


Figure 8: Oxidation of organic matter. Well drained oxidizing environment in which the oxidation of organic matter is the dominant diagenetic process. CO_2 produced via this process has relatively low $\delta^{13}\text{C}$ values (-30‰ to -23‰), similar to those of the organic matter. This is a possible environment for the Blues.

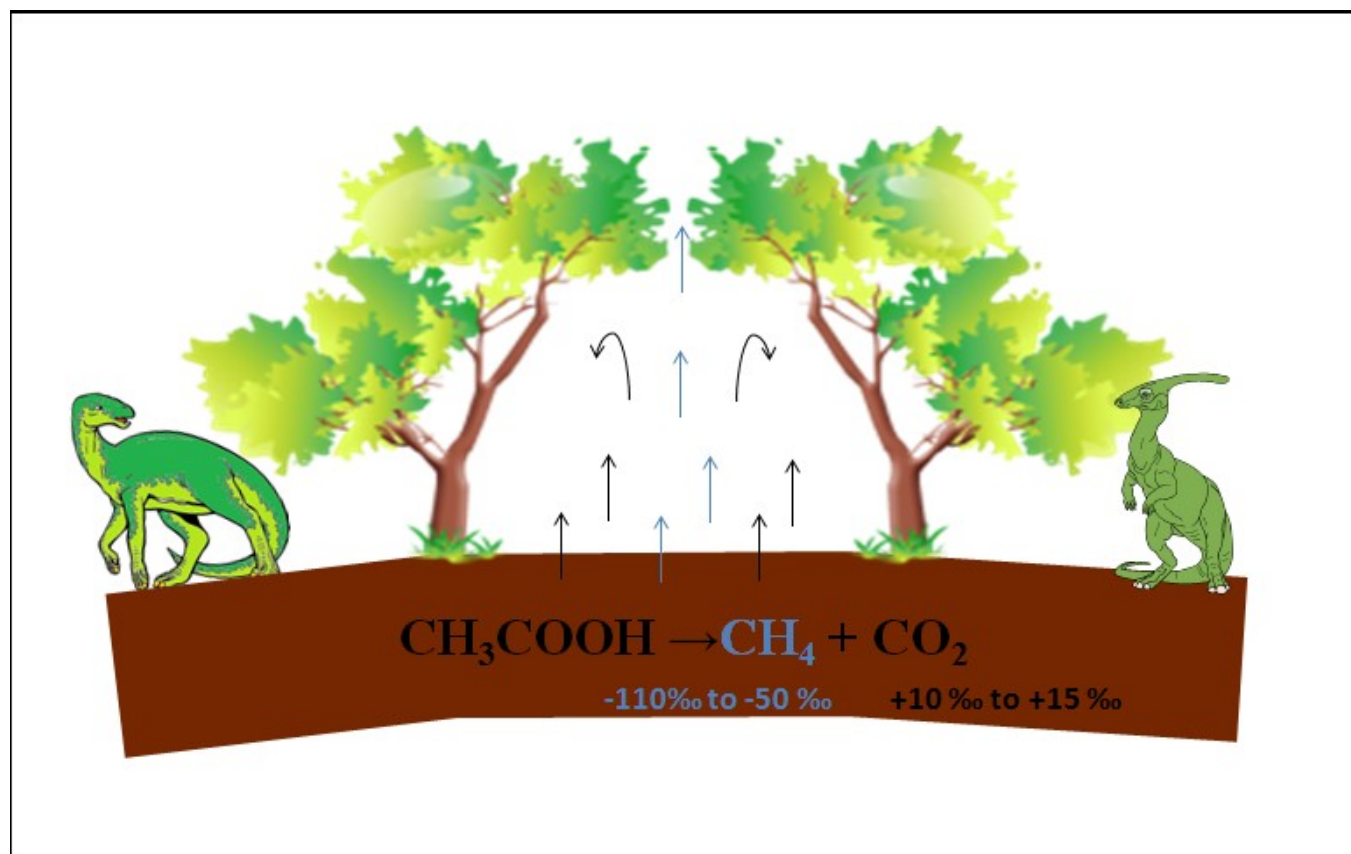


Figure 9: Methanogenesis. Poorly-drained, reducing environment favorable to methanogenesis. The methanogens preferentially incorporate the ^{12}C into the CH_4 , giving it very low $\delta^{13}\text{C}$ (-110‰ to -50‰). The ^{13}C is then incorporated into the CO_2 , giving it very high $\delta^{13}\text{C}$ ($+10\text{‰}$ to $+15\text{‰}$). The CH_4 produced during this process is released into the atmosphere where it can impact the climate of the Late Cretaceous. The CO_2 gets trapped beneath the closed canopy of the forest, where the canopy effect cycles this ^{13}C -enriched CO_2 throughout the forest ecosystem, impacting the $\delta^{13}\text{C}$ of the plants in the forest understory and, potentially, the herbivores that consume them. Comparable to the environment of VCKP2.

6. Conclusion

Although much is known about the Late Cretaceous landscape, many outstanding questions still remain, specifically concerning hadrosaurid behavior, soil processes and forest structure. In an effort to address these outstanding questions, this study undertook a stable isotope analysis of hadrosaurid teeth from three areas that expose the Kaiparowits Formation, focusing on understanding hadrosaurid paleoecology and resource partitioning, paleo-wetland CH₄ production, and the nature of forest structure over Late Cretaceous landscapes of southern Utah.

Comparisons of $\delta^{13}\text{C}$ of tooth enamel from the three locations revealed significant offsets, which indicate that Kaiparowits hadrosaurids were likely occupying two distinct microenvironments characterized by different $\delta^{13}\text{C}$. The difference in $\delta^{13}\text{C}$ could be the result of 1) a difference in dominant plant type, 2) a presence or absence of environmental and climatic stressors, or 3) a presence or absence of closed canopy forests. In addition, the hadrosaurid preferences for these microenvironments were not arbitrary; the occurrence of this isotopic offset suggests that microenvironments were instead partitioned between lambeosaurines and hadrosaurines, with each sub-family utilizing a distinct environment.

Additionally, comparison of $\delta^{13}\text{C}$ of the tooth dentine from the two locations also revealed significant offsets. Since tooth dentine preserves diagenetic isotope signals, this offset indicates the occurrence of different chemical processes taking place within the soil. Elevated $\delta^{13}\text{C}$ provides evidence for the occurrence of bacterial methanogenesis within the soil. Therefore, this study provides the first direct evidence of CH₄ production in Late Cretaceous paleo-wetland environments as a major source of atmospheric CH₄ in

hothouse climates, and proposes that dinosaur tooth dentine can, thus, be used as a proxy for the process of bacterial paleo-methane production.

Finally, the high $\delta^{13}\text{C}$ of hadrosaurid tooth enamel suggests that the ^{13}C -enriched CO_2 produced during methanogenesis is recycled and incorporated into the forest understory by the canopy effect and then consumed by herbivores, including hadrosaurids. This recycling of methanogenically derived CO_2 would suggest the presence of a dense closed canopy forest. Thus, this study provides the first direct evidence that the Kaiparowits alluvial plain hosted a dense closed canopy forest during the Late Cretaceous.

<u>VCKP2 Hadrosaurid Enamel</u>				<u>VCKP2 Hadrosaurid Dentine</u>			
Sample Number	d ¹³ C VPDB	d ¹⁸ O VPDB	d ¹⁸ O VSMOW	Sample Number	d ¹³ C VPDB	d ¹⁸ O VPDB	d ¹⁸ O VSMOW
DMNS 4389 H1E	-6.71	-7.42	23.26	DMNS 4389 H1D	-4.40	-8.37	22.29
DMNS 4389 H2E	-5.92	-8.40	22.25	DMNS 4389 H2D	0.12	-6.80	23.90
DMNS 4389 H5E	-7.33	-9.33	21.29	DMNS 4389 H4D	-2.49	-7.48	23.20
DMNS 4389 H6E	-6.72	-8.26	22.40	DMNS 4389 H5D	-0.94	-7.58	23.09
DMNS 4414 H1E	-4.63	-7.91	22.75	DMNS 4389 H6D	-6.25	-8.55	22.10
DMNS 4414 H3E	-7.34	-7.73	22.94	DMNS 4414 H1D	-3.94	-8.13	22.53
DMNS 4362 H1E	-7.18	-7.23	23.46	DMNS 4414 H2D	-5.99	-10.18	20.42
DMNS 4362 H2E	-6.88	-8.62	22.03	DMNS 4414 H3D	-6.48	-9.96	20.64
DMNS 4362 H3E	-5.45	-7.97	22.70	DMNS 4362 H1D	-2.55	-7.70	22.97
DMNS 4362 H4E	-7.34	-8.08	22.58	DMNS 4362 H2D	-6.83	-8.51	22.14
DMNS 4362 H5E	-5.50	-7.61	23.07	DMNS 4362 H4D	-4.48	-8.07	22.59
DMNS 4418 H1E	-5.80	-8.87	21.76	DMNS 4362 H5D	1.13	-7.74	22.93
DMNS 4418 H2E	-7.39	-8.54	22.11	DMNS 4418 H1D	-6.86	-8.75	21.89
DMNS 4418 H3E	-6.45	-7.81	22.86	DMNS 4418 H2D	-7.24	-8.73	21.92
DMNS 4418 H4E	-7.23	-7.59	23.08	DMNS 4418 H4D	-7.03	-9.47	21.15
DMNS 4418 H5E	-6.50	-8.34	22.31	DMNS 4418 H5D	-2.23	-8.23	22.43
DMNS 4418 H6E	-6.66	-7.78	22.89	DMNS 4418 H6D	-3.04	-8.81	21.83
KPS 13084 H1E	-6.50	-7.82	22.84	KPS 13084 H1D	-0.58	-7.82	22.85
KPS 13030 H1E	-6.75	-8.76	21.88	KPS 13030 H1D	-0.89	-8.37	22.28
KPS 13030 H2E	-6.31	-8.99	21.64	KPS 13030 H2D	-1.30	-8.62	22.02
KPS 13030 H3E	-7.44	-9.02	21.61	KPS 13030 H3D	-3.03	-8.50	22.15
<u>VCKP1 Hadrosaurid Enamel</u>				<u>VCKP1 Hadrosaurid Dentine</u>			
Sample Number	d ¹³ C VPDB	d ¹⁸ O VPDB	d ¹⁸ O VSMOW	Sample Number	d ¹³ C VPDB	d ¹⁸ O VPDB	d ¹⁸ O VSMOW
DMNS 4434 H2E	-7.52	-7.46	23.22	DMNS 4434 H1D	-3.37	-8.22	22.44
DMNS 4434 H3E	-8.45	-7.44	23.24	DMNS 4434 H2D	-7.22	-7.74	22.93
DMNS 4434 H4E	-8.47	-8.59	22.05	DMNS 4434 H3D	-7.43	-7.95	22.72
DMNS 4434 H5E	-7.15	-8.44	22.21	DMNS 4434 H4D	-7.32	-8.44	22.21
DMNS 4434 H6E*	-7.87	-7.68	22.99	DMNS 4434 H5D	-3.40	-8.53	22.12
DMNS 4434 H7E*	-7.60	-7.56	23.12	DMNS 4434 H6D	-6.93	-8.02	22.64
				DMNS 4434 H7D	-7.32	-7.74	22.93
<u>Blues Hadrosaurid Enamel</u>				<u>Blues Hadrosaurid Dentine</u>			
Sample Number	d ¹³ C VPDB	d ¹⁸ O VPDB	d ¹⁸ O VSMOW	Sample Number	d ¹³ C VPDB	d ¹⁸ O VPDB	d ¹⁸ O VSMOW
K-26/FRICKE/K180	-8.52	-8.46	22.19	K1/FRICKE/K180	-7.06	-9.24	21.39
K-27/FRICKE/K180	-8.25	-9.38	21.24	K2/FRICKE/K180	-4.95	-7.99	22.67
K-28/FRICKE/K180	-9.46	-7.33	23.36	K3/FRICKE/K180	-9.01	-8.45	22.20
K-29/FRICKE/K180	-7.54	-9.04	21.59	K4/FRICKE/K180	-6.32	-8.70	21.94
K-30/FRICKE/K180	-9.36	-8.34	22.31	K5/FRICKE/K180	-9.04	-8.65	21.99
K-31/FRICKE/K180	-9.01	-8.80	21.84	K6/FRICKE/	-7.37	-8.59	22.06
K-32/FRICKE/K180	-8.59	-7.55	23.13	K7/FRICKE/K180	-7.36	-8.29	22.36
K-33/FRICKE/K180	-8.65	-7.75	22.92	K8/FRICKE/K180	-5.99	-8.62	22.02
K-34/FRICKE/K180	-8.99	-6.89	23.81	K9/FRICKE/K180	-5.67	-8.52	22.13
K-35/FRICKE/K180	-9.34	-9.61	21.00	K10/FRICKE/K180	-7.89	-9.90	20.70
K-36/FRICKE/K180	-8.15	-8.07	22.59	K11/FRICKE/K180	-6.86	-8.36	22.30
K-37/FRICKE/K180	-8.80	-8.62	22.03	K12/FRICKE/K180	-8.32	-8.02	22.65
K-38/FRICKE/K180	-7.64	-7.10	23.59	K13/FRICKE/K180	-4.28	-7.64	23.04
K-39/FRICKE/K180	-8.06	-7.98	22.68	K14/FRICKE/K180	-5.72	-8.30	22.36
K-40/FRICKE/K180	-9.14	-8.84	21.80	K15/FRICKE/K180	-8.46	-8.32	22.33
DMNS 4173 H1E	-7.55	-8.07	22.59	DMNS 4173 H1D	-1.84	-8.09	22.57
DMNS 4173 H2E	-7.22	-7.14	23.55	DMNS 4173 H2D	-0.81	-7.62	23.06
DMNS 4173 H3E	-9.38	-7.13	23.55	DMNS 4173 H5D	-4.72	-8.09	22.57
DMNS 4173 H4E	-9.13	-8.63	22.01				

Table 1: Stable isotope ratios for hadrosaurid enamel and dentine for the Kaiparowits Formation.

Variable 1	Variable 2	p value	F test conclusion	p value	T test conclusion
VCKP2 hadro enamel oxygen	VCKP2 hadro dentine oxygen	0.0827	not different	0.352952	not different
VCKP2 hadro enamel carbon	VCKP2 hadro dentine carbon	3.36E-07	different	4.68E-05	different
VCKP1 hadro enamel oxygen	VCKP1 hadro dentine oxygen	0.130392	not different	0.350287	not different
VCKP1 hadro enamel carbon	VCKP1 hadro dentine carbon	0.006794	different	0.056821	not different
Blues hadro enamel oxygen	Blues hadro dentine oxygen	0.048228	different	0.245991	not different
Blues hadro enamel carbon	Blues hadro dentine carbon	4.5E-06	different	0.000427	different
VCKP1 hadro enamel oxygen	Blues hadro enamel oxygen	0.160477	not different	0.436766	not different
VCKP1 hadro enamel carbon	Blues hadro enamel carbon	0.271002	not different	0.031164	different
VCKP1 hadro enamel oxygen	VCKP2 hadro enamel oxygen	0.429218	not different	0.219172	not different
VCKP1 hadro enamel carbon	VCKP2 hadro enamel carbon	0.220288	not different	0.000787	different
VCKP2 hadro enamel oxygen	Blues hadro enamel oxygen	0.075483	not different	0.818179	not different
VCKP2 hadro enamel carbon	Blues hadro enamel carbon	0.390133	not different	2.07E-10	different
Blues hadro dentine carbon	VCKP2 hadro dentine carbon	0.277372	not different	0.002211	different
Blues hadro dentine carbon	VCKP1 hadro dentine carbon	0.337102	not different	0.952005	not different
VCKP2 hadro dentine carbon	VCKP1 hadro dentine carbon	0.21049	not different	0.025939	different

Table 2: Results of statistical analyses. F -tests and t-tests.

Acknowledgements

I would like to thank: Dr. Henry Fricke for giving me the opportunity to work with the Denver Museum of Nature and Science (DMNS) and for advising me, assisting me with revisions, and guiding me through the thesis writing process; the trustees of the Rocky Mountain Association of Geologists Foundation for the Philip J. McKenna Scholarship; the Patricia Buster Research Scholarship Fund for the Buster Stipend and Grant; DMNS for loaning me the hadrosaurid teeth used for this study. I would also like to thank Dr. Joe Sertich, Dr. Ian Miller, Dr. Scott Sampson, Carol Lucking, Dr. Logan Ivy, Dr. Mike Getty, Doug Kline and other DMNS employees and volunteers for teaching and mentoring me and giving me the opportunity to join them in the field in Wyoming and at the Kaiparowits; the University of Arizona for stable isotope analysis. Additionally, I would like to acknowledge Dr. Steve Getty and Dr. David Brown for help with statistics and graphing; Ashley Randle, Kiyomi Moore, Alyssa Fortune and Arianna Gentile Polese for occasional wording and spelling advice; Dr. Paul Myrow, Brenna Swift and Joe and Jane Crystal for editing and revision assistance; the workers at the Colorado College CAT Lab for assistance with creating figures; and, finally, the Colorado College Geology Department for teaching, supporting and guiding me throughout the past four years.

References

- Beerling, D., Berner, R. A., Mackenzie, F. T., Harfoot, M. B., and Pyle, J.A., 2009, Methane and the CH₄-related greenhouse effect over the past 400 million years: *American Journal of Science*, v. 309, no. 2, p. 97-113, doi: 10.2475/02.2009.01.
- Beerling, D. J., Fox, A., Stevenson, D. S., and Valdes, P. J., 2011, Enhanced chemistry-climate feedbacks in past greenhouse worlds: *PNAS*, v. 108, n. 24, p. 9770-9775, doi: 10.1073/pnas.1102409108.
- Blakey, R., 2011, Late Cretaceous (75 Ma), NAU Geology, <http://jan.ucc.nau.edu/rcb7/nam.html>.
- Bowen, G. J. and Bloch, J. I., 2002, Petrography and geochemistry of floodplain limestones from the Clarks Fork Basin, Wyoming, U.S.A.: Carbonate deposition and fossil accumulation on a Paleocene-Eocene floodplain: *Journal of Sedimentary Research*, v. 72, no. 1, p. 46-58.
- Carrano, M. T., Janis, C. M., and Sepkoski, J. J., Jr., 1999, Hadrosaurs as ungulate parallels: lost lifestyles and deficient data: *Acta Palaeontologica Polonica*, v. 44, p. 237-261.
- DeConto, R. M., Brady, E. C., Bergengren, J., and Hay, W. W., 2000, Late Cretaceous climate, vegetation and ocean interactions; Pp. 275-296 in B. T. Huber, K. G. MacLeod, and S. L. Wing, eds. *Warm Climates in Earth History*: Cambridge, United Kingdom, Cambridge University Press, 462 p.
- Diefendorf, A. F., Mueller, K. E., Wing, S. L., Koch, P. L., and Freeman, K. H., 2010, Global patterns in leaf ¹³C discrimination and implications for studies of past and future climate: *Proceedings of the National Academy of Sciences*, v. 107, no. 13, p. 5738-5743.
- Drucker, D. G., Bridault, A., Hobson, K. A., Szuma, E., and Bocherens, H., 2008, Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 266, p. 69-82, doi: 10.1016/j.palaeo.2008.03.020.
- Eberth, D. A., Rogers, R. R., and Fiorillo, A. R., 2007, A practical approach to the study of bonebeds; Pp. 265-332 in Rogers, R. R., Eberth, D. A., Fiorillo, A. R., eds. *Bonebeds: genesis, analysis and paleobiological significance*: Chicago, Illinois, University of Chicago Press, 512 p.

- Fastovsky, D. E. and Smith, J. B., 2004, Dinosaur Paleoecology; Pp. 614-626 *in* Weishampel, D. B., Dodson, P., and Osmolska, H., eds. *The Dinosauria*: Berkeley, CA, University of California Press, 861 p.
- Fletcher, B. J., Brentnall, S. J., Anderson, C. W., Berner, R. A., Beerling, D. J., 2008, Atmospheric carbon dioxide linked with Mesozoic and early Cenozoic climate change: *Nature Geoscience*, v. 1, p. 43-48, doi: 10.1038/ngeo.2007.29.
- Fricke, H. C., and Pearson, D. A., 2008, Stable isotope evidence for changes in dietary niche partitioning among hadrosaurian and ceratopsian dinosaurs of the Hell Creek Formation, North Dakota: *Paleobiology*, v. 34, no. 4, p. 534–552, doi: 10.1666/08020.1.
- Fricke, H. C., Rogers, R. R., Backlund, R., Dwyer, C. N., and Echt, S., 2008, Preservation of primary stable isotope signals in dinosaur remains, and environmental gradients of the Late Cretaceous of Montana and Alberta: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 266, no. 1-2, p. 13- 27, doi: 10.1016/j.palaeo.2008.03.030.
- Fricke, H. C., Rogers, R. R., and Gates, T. A., 2009, Hadrosaurid migration: inferences based on stable isotope comparisons among Late Cretaceous dinosaur localities: *Paleobiology*, v. 35, no. 2, p. 270–288, doi: 10.1666/08025.1.
- Fricke, H. C., Foreman, B. Z., and Sewall, J. O., 2010, Integrated climate model-oxygen isotope evidence for a North American monsoon during the Late Cretaceous: *Earth and Planetary Science Letters*, v. 289, no. 1, p. 11-21.
- Gates, T. A., Sampson, S. D., Zanno, L. E., Roberts, E. M., Eaton, J. G., Nydam, R. L., Hutchinson, J. H., Smith, J. A., Loewen, M. A., and Getty, M. A., 2010, Biogeography of terrestrial and freshwater vertebrates from the late Cretaceous (Campanian) Western Interior of North America: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 291, p. 371–387, doi:10.1016/j.palaeo.2010.03.008.
- Heaton, T. H. E., 1999, Spatial, species and temporal variations in the $^{13}\text{C}/^{12}\text{C}$ ratios of C_3 plants: implications for paleodiet studies: *Journal of Archaeological Science*, v. 26, p. 637-649.
- Huber, B. T., 1998, Tropical paradise at the Cretaceous poles: *Science*, v. 282, no. 5397, p. 2199-2200, doi: 10.1126/science.282.5397.2199.
- Irwin, H., Curtis, C., Coleman, M., 1977, Isotopic evidence for source of diagenetic carbonates formed during burial of organic-rich sediments: *Nature*, v. 269, p. 209-213.

- Jahren, A. H., LePage, B. A., and Werts, S. P., 2004, Methanogenesis in Eocene Arctic soils inferred from $\delta^{13}\text{C}$ of tree fossil carbonates: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 214, p. 347-358, doi:10.1016/j.palaeo.2004.07.030.
- Koch, P. L., 1998, Isotopic reconstruction of past continental environments: Annual review of Earth and Planetary Sciences, v. 26, p. 573-613.
- Kohn, M. J. and Cerling, T. E., 2002, Stable isotope compositions of biological apatite: *Reviews in Mineralogy and Geochemistry*, v. 48, no. 1, p. 455-488.
- Lehman, T. M., 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. *Proceeding of the DinoFest International symposium Arizona State University: Philadelphia, Academy of Natural Sciences*, p. 587.
- Lehman, T. M., 2001, Late Cretaceous dinosaur provinciality; Pp. 310-328 *in* D. Tanke and K. Carpenter, eds. *Mesozoic vertebrate life: Bloomington, Indiana, Indiana University Press*, 577 p.
- Miller, I., 2014, Personal Communication.
- Miller, I. M., Johnson, K. R., Kline, D. E., Nichols, D. J., and Barclay, R. S., 2013, A Late Campanian flora from the Kaiparowits Formation, Southern Utah, and a brief overview of the widely sampled but little-known Campanian vegetation of the Western Interior of North America; Pp. 107- 131 *in* A. L. Titus and M. A. Loewen, eds. *At the top of the Grand Staircase: the Late Cretaceous of Southern Utah: Bloomington and Indianapolis, Indiana, Indiana University Press*, 656 p.
- Pang, M., and Nummedal, D., 1995, Flexural subsidence and basement tectonics of the Cretaceous Western Interior basin, United States: *Geology*, v. 23, no. 2, p. 173-176.
- Roberts, E. M., Deino, A. L., and Chan, M. A., 2005, $^{40}\text{Ar}/^{39}\text{Ar}$ 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*, v. 26, no. 2, p. 307-318, doi: 10.1016/j.cretres.2005.01.002.
- Roberts, E. M., 2007, Facies architecture and depositional environments of the Upper Cretaceous Kaiparowits Formation, southern Utah: *Sedimentary Geology*, v. 197, no. 3-4, p. 207-233, doi: 10.1016/j.sedgeo.2006.10.001.

- Roberts, E. M., Sampson, S. D., Deino, A. L., Bowring, S. A., Buchwaldt, R., 2013, The Kaiparowits Formation: a remarkable record of Late Cretaceous terrestrial environments, ecosystems, and evolution in Western North America; Pp. 85-106 *in* A. L. Titus and M. A. Loewen, eds. *At the top of the Grand Staircase: the Late Cretaceous of Southern Utah: Bloomington and Indianapolis, Indiana*, Indiana University Press, 656 p.
- Sampson, S. D., Loewen, M. A., Roberts, E. M., and Getty, M. A., 2013, A new macrovertebrate assemblage from the Late Cretaceous (Campanian) of Southern Utah; Pp. 599-620 *in* A. L. Titus and M. A. Loewen, eds. *At the top of the Grand Staircase: the Late Cretaceous of Southern Utah: Bloomington and Indianapolis, Indiana*, Indiana University Press, 656 p.
- Schouten, S., Woltering, M., Rijpstra, I. C., Sluijs, A., Brinkhuis, H., and Sinninghe Damsté, J. S., 2007, The Paleocene–Eocene carbon isotope excursion in higher plant organic matter: Differential fractionation of angiosperms and conifers in the Arctic: *Earth and Planetary Science Letters*, v. 258, p. 581-592.
- Sewall, J. O., and Fricke, H. C., 2013, Andean-scale highlands in the Late Cretaceous Cordillera of the North American western margin: *Earth and Planetary Science Letters*, v. 362, p. 88-98, doi: 10.1016/j.epsl.2012.12.002.
- Upchurch, G. R., Jr., and Wolfe, J. A., 1993, Cretaceous vegetation of the Western Interior and adjacent regions of North America: *Geological Association of Canada Special Paper*, v. 39, p. 243-281.
- Van de Water, P. K., Leavitt, S. W., and Betancourt, J. L., 2002, Leaf $\delta^{13}\text{C}$ variability with elevation, slope aspect, and precipitation in the southwest United States: *Oecologia*, v. 132, p. 332-343, doi: 10.1007/s00442-002-0973-x.
- Van der Merwe, N. J. and Medina, E., 1991, The canopy effect, carbon isotope ratios and foodwebs in Amazonia: *Journal of Archaeological Science*, v. 18, p. 249-259.
- Whiticar, M. J., 1999, Carbon and hydrogen isotope systematic of bacterial formation and oxidation of methane: *Chemical Geology*, v. 161, p. 291-314.
- Wing, S. L. and Boucher, L. D., 1998, Ecological aspects of the Cretaceous flowering plant radiation: *Annual Review of Earth and Planetary Sciences*, v. 26, no. 1, p. 379-421.
- Wing, S. L. and Tiffney, B. H., 1987, The reciprocal interaction of angiosperm evolution and tetrapod herbivory: *Review of Palaeobotany and Palynology*, v. 50, p. 179-210.

Wing, S. L., Strömberg, C. A. E., Hickey, L. J, Tiver, F., Willis, B., Burnham, R. J., Bhrensmeier, A. K., 2012, Floral and environmental gradients on a Late Cretaceous landscape: *Ecological Monographs*, v. 82, no. 1, p. 23-47.

Wolfe, J. A. and Upchurch, G. R., Jr., 1987, North American nonmarine climates and vegetation during the Late Cretaceous: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 61, p. 33-77.