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The Association Between Dietary Niche Variation in Rodents and Climate Change Across the Paleocene-Eocene Thermal Maximum

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The Association Between Dietary Niche Variation in Rodents and Climate Change Across the
Paleocene-Eocene Thermal Maximum

Hannah K. Vermeer

A Thesis Submitted to the Graduate Faculty of

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Abstract

Mammalian teeth play a crucial role in food acquisition and breakdown and are therefore closely tied to dietary niche. This study reconstructed the diet of early Paleogene paramyid rodents across the Paleocene-Eocene Thermal Maximum (PETM) climatic event in an effort to understand the role of climate in mammalian dietary niche change. Dietary niches were quantified using three dental topographic measures: Dirichlet normal energy, relief index, and orientation patch count rotated. A Kruskal-Wallis test was conducted over eight time periods to determine if each of the dental topographic measures (i.e., diet) varied over time. Regression analysis of these measures with climatic variables was then used to evaluate the relationship of dietary niche with climate change. Results from the Kruskal-Wallis test indicated dietary niche variation over time ($P=0.005$) for the Dirichlet normal energy topographic measurement; however, regression analysis results did not indicate an association between dietary niche in these paramyid rodents and climate change across the time periods studied. While overall the results indicate that paramyid rodents likely experienced some dietary niche variation across the PETM, this study rejects the hypothesis that this variation is associated with the known climate change of this time. It is possible that the ability of paramyid rodents to utilize a large range of food resources resulted in a lack of competition for resources from mammalian immigrants and may have limited their need for significant dietary niche change in response to the PETM.

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Abbreviations:

PETM: Paleocene-Eocene Thermal Maximum

NALMA: North American Land Mammal Age

DNE: Dirichlet Normal Energy

RFI: Relief Index

OPCR: Orientation Patch Count Rotated

MAT: Mean Annual Temperature

MANOVA: multivariate analysis of variance

Introduction

Dentition and Dietary Niche

The mammalian fossil record is a valuable tool used by scientists, allowing opportunities to learn not only about what existed in the world long ago but also how evolutionary change has shaped the world into what we know today (1,2). The mammalian fossil record includes an abundance of teeth and jaws (3), making it a wealth of information on evolutionary change of individual mammalian taxa and mammalian communities as a whole. The focus of the following research is on fossils of Paleogene mammalian, particularly paramyid rodent, dentitions.

Mammalian teeth are complex and composed of several components (4,5). The basic structure of a mammalian tooth is typically a crown covered by a layer of enamel, and a root that is covered in cementum. Enamel and cementum are mineralized tissues, with enamel providing a hard coating around the dentin, and cementum covering the root(s) of the tooth (6). The dentin found deep to the enamel encompasses the pulp. The pulp is located in the center of the tooth and contains nerves and blood vessels that run through the root canals and maintain the tooth.

Mammalian teeth are contained within sockets in the mandible, maxilla, and premaxilla, held in place by ligaments that provide sensory feedback on the movement of the teeth. This feedback is important in the movements that lead to mastication (5).

As teeth play a critical role in mammalian food acquisition and breakdown, much can be learned by studying their shape (7). With a variety of possible roles, tooth shape is closely tied to function (8), and as such, shape is determined by a tooth's location in the mouth and associated with the type of food it breaks down (9). During mastication, food follows a pattern of movement provided by the teeth and determined by the type of breakdown required. Food items must first be gripped by the teeth. Following grip, the food item can either be transported by the tongue, or

if further breakdown is needed, fracture occurs. Most mammals require teeth to fracture their food items (9). After fracture, food items may be further reduced by sculpture to reach a desired particle shape before transport by the tongue, or they may be further reduced by comminution if no specific shape is required (9). Further descriptions of these actions can be found in Table 1.

Table 1. Roles of dentition and their descriptions. (9)

Role of Dentition	Description
Grip	Requires friction to hold food particles. During transport, grip may involve crack initiation.
Fracture	Beginning stage of food particle breakdown
Sculpture	Further food particle size reduction and specific shaping strategy exhibited by some mammals
Comminution	Repeated food particle size reduction strategy used if a specific shape is not required

Mammalian teeth are categorized into several different types: incisors, canines, premolars, and molars (4). Incisors, located anteriorly, are often chisel-like. This tooth type typically has one cusp and one root and is used in gripping and scraping. The overall role of incisors is to introduce food into the mouth in small pieces to be further broken down by other teeth. Canines are found distal to the incisors. Like incisors, canines normally have one root and one cusp. They are characterized by sharp edges used for biting and holding prey. Premolars are found distal to the canines and may vary greatly in size and shape. Molars are found most distally in the mouth and, like the premolars, they display large variation in size and crown shape (10). The role of molars and premolars is to break down food particles into smaller pieces by crushing, grinding, or slicing (5).

Because the teeth are responsible for food breakdown, the structure and function of the dentition of any particular mammal is closely tied with that mammal's dietary niche. Here, a dietary niche refers to the food resources available and used by an organism for survival (11).

Many mammalian diets consist of their food preferences, as well as foods that they are willing to consume (5). Diet may change depending on availability of resources due to seasonality, climate change, or other factors that may lead to a difference in available food resources.

Mammalian dietary niches can be categorized by the main components that make up the diet. Traditionally, mammalian diets are classified by the following feeding strategies: carnivorous (meat eater), herbivorous (plant eater), and omnivorous (both meat and plant eater) (12). These classifications, however, are broad and do not demonstrate the differences that can be found within each category. A further breakdown of these categories can be found in Table 2.

Table 2. Dietary niche classification as described by Ref. 12.

Dietary Characterization	Description	Example	Food Source
Carnivore	Meat eater	Insectivore	Insects
Herbivore	Plant eater	Granivore	Seeds
		Frugivore	Fruit
		Folivore	Leaves
		Nectarivore	Nectar
		Gummivore	Exudate Gums
Omnivore	Meat and plant eater	-	

The dental morphology observed in a mammal provides information on its dietary niche (13). This is especially important in extinct mammals, as information can be gleaned by studying different aspects of fossil teeth, such as the arrangement of cusps on occlusal surfaces of molars (14). Specific dental morphologies are necessary for masticatory efficiency (15), with the end goal of mastication being proper mechanical breakdown leading to efficient uptake of nutrients (15).

Thus, mammalian tooth morphology is correlated with the biomechanical properties of the foods they break down (15,16). Proper mechanical breakdown of food items requires dentition that is suitable for a given dietary niche. Some animals have dietary niches that require dentition that is well suited for crushing, where crushing surfaces are found perpendicular to the force applied, and the borders of the crushing area are walled to avoid food escape (17). This dentition would be utilized by a mammal that processes a diet of fruits or nuts, and differs from the dentition needed by a mammal that breaks down insects or cellulose-rich items, like leaves (11). These latter dietary items would require dentition suitable for shearing, which is done by the leading edges of the crests on the crowns of the post-canine dentition (17).

As tooth form and function has been linked as a factor in determining dietary niche (2,11,15), researchers have developed several methods for dental analysis. Quantitative analysis of the three-dimensional structure of teeth is particularly useful in these studies, and dental topography provides a measurable variable for quantitative study (11). In the case of extinct mammals, all the information about their diet must come from the fossils they leave behind. Dental topography has been demonstrated to reflect dietary niche variation (18,19), and provides a quantitative method for studying dental fossils to understand dietary niche.

Quantitative Analysis of Dental Morphology

Quantitative analysis of dental morphology may be carried out by taking three-dimensional images of teeth to obtain measurements from which to study the surfaces of those teeth (11,20,21). These dental topographic measures represent a three-dimensional tooth using a single metric (16), giving a quantitative result that can then be utilized to study different aspects of that tooth. Currently, several methods are used to quantitatively predict dietary niche.

One method for analyzing dental morphology is Dirichlet normal energy (DNE). DNE uses measurements to quantify the curvature of a surface (22). This method can be applied to the occlusal surface of a tooth, producing a mathematical value for the curvature of that occlusal surface (22). Higher DNE values indicate an increase in curvature (21), resulting in a tooth that is sharper and potentially better suited for efficient fracturing of food items (16). Sharper teeth are well-suited for shearing and are indicative of an insectivorous or folivorous diet (11), whereas teeth with low curvature, resulting in low DNE values, are indicative of an omnivorous or frugivorous diet. This method has been used to study dental topography in lemurs (21), stem primates (22), and to study dietary niche overlap of primates and rodents (11).

Relief index (RFI) is another method of analysis that has been used to study dietary niche and is the ratio of a tooth crown's three-dimensional area to its two-dimensional planar area (23). This measure is the ratio of the square roots of the surface area of the enamel crown and the surface area of the crown's projection onto an occlusal plane. RFI is a measure of topography relative to the occlusal plane. For this measurement, higher values indicate more tooth surface available for contact with food items (16). Like DNE, higher RFI values indicate an insectivorous or folivorous diet, and lower values indicate a frugivorous diet (11). In his research on second mandibular molars and diet among euarchontans, Boyer (2008) found RFI to be a useful measurement for dietary reconstruction and differentiation, as variance in RFI can be attributed to dietary diversity (20). In addition to Boyer's (2008) work on euarchontans, RFI has been previously used to study dental topography of Neotropical primates as well as rodents (11,19).

Orientation patch count rotated (OPCR) is a third dental topographic measurement in common use, and is utilized to measure the complexity of the occlusal surface of a tooth. As a

result, this measurement provides a quantitative value which is used to determine the complexity of that surface (11,21). Orientation patch counts increase as the complexity of an occlusal surface increases (21), which tends to be the case with teeth exhibiting more cusps or enamel crenulations (11). OPCR values are typically highest in herbivores and lowest in carnivores (18). OPCR has been used to study dental complexity in primates, rodents, and carnivorans (11,18).

Bunn et al. (2011) studied the use of five dental topographic measurements, including DNE, RFI, and OPCR, on extant primate samples, finding DNE and RFI to be closely correlated with diet (24). This research also found that while OPCR was the least effective metric for predicting diet on its own, there is still value in this measurement to predict dietary complexity. This is because it was the only quantitative measurement of surface complexity and is a useful metric when used in combination with DNE and RFI (24). Winchester et al. (2014) also found a high rate of success in dietary prediction of prosimians when combining these methods to study second mandibular molars (19).

The dental topographic measurements mentioned utilize different aspects of a tooth's surface to quantify elements related to the function of that tooth. The studies mentioned above have applied one or more of these methods to study dietary niches using dental samples, primarily second mandibular molars. The resulting analysis has given researchers insight into dental similarities (18), competition (22), and overall dietary niche and dietary niche changes (19–22) in mammals.

Bighorn Basin and Paleogene Rodents

The Bighorn Basin is well-known as a wealth of plant and mammalian fossils that document the Paleocene-Eocene transition ca. 56 Ma in North America (25). Located in north-western Wyoming, the abundance of fossils in this area enables researchers to glimpse into how

this community has evolved over time. Of particular interest are the fossils of numerous mammalian species that have been found in this location (26). The contribution of these fossils to the mammalian fossil record afford the opportunity to study faunal turnover and diversity as well as how these factors helped shape the evolution of these groups across the Paleogene (1). The group of mammalian fossils found in the Bighorn Basin that is the focus of this research belong to the order Rodentia.

Rodents are diverse and abundant, making up more than one-third of all living mammalian species (27,28). Rodents can be distinguished by their anterior dentition being comprised of only one pair of upper and lower incisors (29), which are large, self-sharpening (30), and continue to grow throughout their lifetime (26,28). These mammals feed by either using their incisors to gnaw, or by using their molars to chew, but are incapable of using both methods simultaneously due to a difference in cranial and mandibular length (30). This research focused specifically on one family from the order Rodentia: Paramyidae.

Paramyids are among the oldest and most primitive known fossil rodents and are found as early as the Clarkforkian (31–34). Though some data has been gleaned from limited postcranial fossils of paramyids, most of the information available on the anatomy of these early rodents is based on craniodental remains (27). This is due to the quantity and quality of the dental samples from paramyid fossils (22), making dentition the focus of studies on this family of rodents (33). The dental formula for paramyids is $I^1_1, C^0_0, P^2_1,$ and M^3_3 , where I = incisor, C = canine, P = premolar, and M = molar (33).

Paramyids are medium- to large-sized rodents (35) and are most similar to squirrels, with traits that resemble those of both extant tree squirrels and ground squirrels (27). Early Eocene paramyids are thought to have foraged at or near ground level (36), though it is presumed that

different habitats were occupied by the various members of this family (33). Additionally, studies on the masticatory adaptations of paramyids suggest they were omnivorous (37).

As discussed previously, rodents first appear in the fossil record in the late Paleocene, with fossils of Paramyidae found from the Clarkforkian of western North America (27). The North American Paleocene-Eocene stratigraphic record is divided into North American Land Mammal Ages (NALMAs), and further broken down into sub-North American Land Mammal Ages (sub-NALMAs) (1). This research focused on two of these NALMAs, the Clarkforkian (Cf2-3; end of the Paleocene, ~56.5-55.8 Ma) and the Wasatchian (Wa0-5; beginning of the Eocene, ~55.8-53.9 Ma) in the Bighorn Basin of Wyoming, spanning from sub-NALMAs Cf2 through Wa5. A breakdown of time periods involved in this study can be found in Figure 1 below.

Figure 1. Time scale used for this study. NALMA: North American Land Mammal Age. Time periods from Chew and Oheim (2013) and Secord et al. (2006) (38,39).

Sub-NALMA											
	Cf2		Cf3		Wa0 Wa1-2		Wa3 Wa4		Wa5		
Ma	56.5		56.0		55.5		55.0		54.5		54.0

Climate

The Paleocene-Eocene Thermal Maximum (PETM), ca. 55.8 Ma, was a time of rapid global warming, as well as biotic events that included changes in the taxonomic and trophic composition of terrestrial vertebrate faunas (38,40–42). Researchers have determined temperatures of this time by obtaining estimates of mean annual temperature (MAT) from fossil land plants (25), giving a broader picture of the Bighorn Basin at the Paleocene-Eocene

boundary. MAT changed across the late Paleocene through the middle Eocene. An initial rise in MAT occurred during the Clarkforkian, up from 13°C at the beginning to a peak of 18°C at the end of the Clarkforkian (25). At the beginning of the Wasatchian, MAT was 18°C, which fell to 11°C in the middle of the Wasatchian (25). This temperature peak occurring across the Paleocene-Eocene boundary is known as the PETM. Research conducted on paleosols from the Bighorn Basin has indicated climatic drying at the beginning of the PETM, with precipitation increasing throughout the roughly 100,000-year event (41).

In addition to obtaining climate information from fossil plants and paleosols, climate change research has also included studies on deep sea oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotopes (43). The resulting high-resolution datasets have played an important role in reconstructing global climate change, with oxygen isotopes serving as a proxy for temperature and carbon isotopes serving as a proxy for precipitation (43). The results of these data indicate a deep-sea temperature increase of 5-6°C across the PETM, associated with globally higher humidity and precipitation (43).

Information from flora in Wyoming, USA across the PETM is also available, due to the fossil record. These fossil records indicate a floral response to the warming during the PETM, with large shifts in plant ranges over a 10,000 year period (40). Immigrant plant species from the south and east of North America and from Europe were found, in addition to plant species native to this area (40). The number of plant species found in this area peaked at ~40 species at the beginning of the Clarkforkian, with a rapid decline to ~26 species during the warming that occurred during the Paleocene-Eocene boundary (25).

Evidence also suggests that significant mammalian community reorganization occurred in North America during the PETM as a result of the global warming taking place, seen in

geographic redistributions of species (44). According to research by Woodburne et al. (2009), a global temperature increase of $\sim 5^{\circ}\text{C}$ led to an increase in first appearances of mammals due to climate-induced immigration (45), with research by Clyde et al. (1998) documenting 15 first appearances during Wa0 (42). In addition to the mammalian reorganization, Maas et al. (1995) identified 4 intervals of significant faunal change over the middle Paleocene through the early Eocene in the Bighorn Basin, two of which were found in the Wasatchian (1).

The period of climate change during the Wasatchian was also a time of significant generic turnover that resulted in an increase in generic richness (1). Climate change has been suggested to have an impact on biotic interactions, such as competition (46). Understanding the link between climate change and reconstructed rodent dietary niche may give insight into changes in interactions between rodents and other mammals. For example, did dietary niche variation result in new competition for resources, and what impact could this have had on the changes in generic turnover and richness observed during this time?

Relevance and Hypotheses

According to Gingerich (2004), “One of the most fundamental and important questions about evolution in any group of organisms is the degree to which it responds to environmental change” (47). Environmental change over the Clarkforkian and Wasatchian in the Bighorn Basin is well-documented, but it is also important to understand how the environmental changes that have been observed correspond to aspects of mammalian life, such as dietary niche transitions over generations.

Teeth offer a glimpse into the dietary niches of fossil mammals, as dental topographic analysis may be used to reconstruct diet from molars (21,48–50). Understanding dietary niche is important because the food resources that a mammal consumes is a primary ecological parameter

that can be used to understand evolutionary history (20). Dietary variance is suggested to have significant effects on aspects of the lives and morphologies of mammals (51), and diet is therefore an important and well-studied aspect of paleontological (and neocological) research (2).

Combining information on the dietary niche of extinct mammals with patterns of climate change that took place at the same time can help determine the impact climate change had (if any) on interactions amongst those mammals (specifically rodents in the case of this research). Additionally, it can also be used to study how these changes affected the interactions of these rodents with other mammals of their time. This information is important to understanding the patterns of past change and how those patterns could be applied to understanding future changes in mammalian species and communities as a result of climate shifts (46).

The goal of this research is to use dental topographic measurements to determine if dietary niche change in paramyids from the Bighorn Basin occurred across eight sub-NALMAs from the late Paleocene through the early Eocene. The expectation is that changes in dietary niche (reconstructed from dental topographic measures) will be observed over the time periods studied (Hypothesis 1). The results obtained from the dental specimens will then be compared to known data on climate during this time. The expectation is that dietary niche change will be associated with reconstructed climate change during this time period (Hypothesis 2).

Materials and Methods

Study Area

This study was conducted on a sample of members of the family Paramyidae of the order Rodentia from the Bighorn Basin. The Bighorn Basin is located in Wyoming, USA and is the site of an abundant collection of Paleogene fossils.

Rodentia Samples

The samples used in this study comprises 93 μ CT-scanned first or second mandibular molars of paramyids from the Bighorn Basin, spanning the Cf2 to Wa5 sub-NALMAs. A breakdown of specimens over the eight sub-NALMAs is detailed in Table 3 below.

Table 3. Bighorn Basin specimens included in this study. Time period assignments are from Clarkforkian (Cf2) through Wasatchian (Wa5), ca. 56.5-53.9 Ma (37,38). N = number of specimens.

Time Period	N
Cf2	7
Cf3	4
Wa0	8
Wa1	13
Wa2	16
Wa3	13
Wa4	14
Wa5	18
Total	93

Specimen Collection and μ CT-Scanning

The sample was collected by Dr. Laura Stroik and consists of 93 μ CT-scanned first or second mandibular molars. To obtain the μ CT scans, impressions of dentitions were taken,

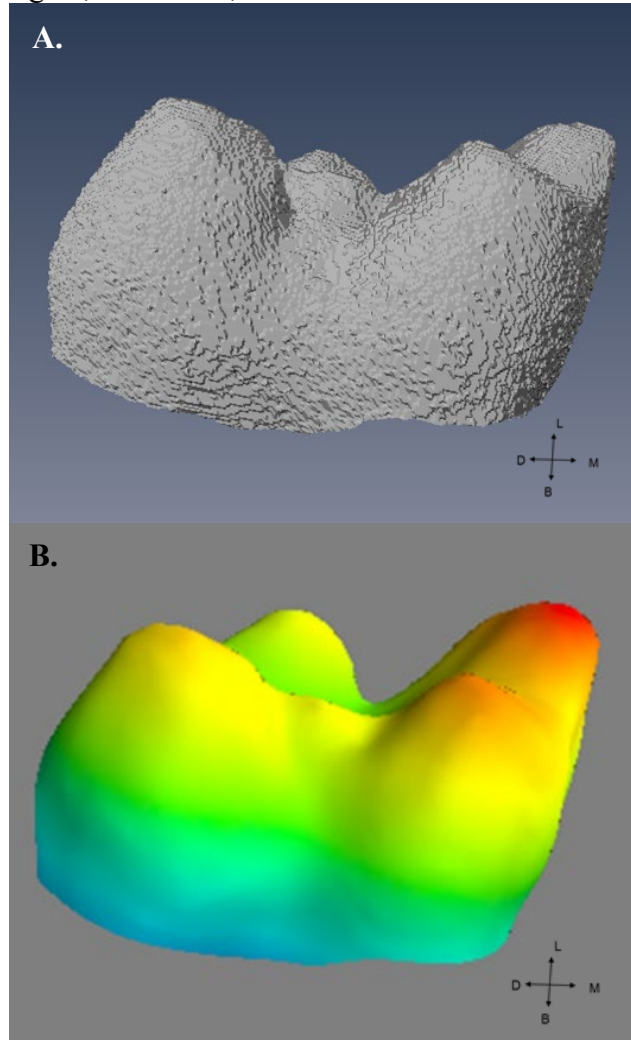
molded, and cast by Dr. Stroik. Casts of the first or second mandibular molars were then excised and arranged in groups on a 1-inch diameter wafer. Wafers were set up in towers and sent to the Duke University Shared Materials Instrumentation Facility (SMiF) to be μ CT-scanned. μ CT-scanning was conducted using a NIKON XT 225 ST micro x-ray computed tomography scanner to obtain high resolution images of the surfaces of the teeth, creating a radiographic image. This process yields high resolution topographic images, which are useful in studying the surfaces of small dental specimens.

Scan Processing and MorphoTester

Amira software (version 5.2.0) was used in this study. In this software, the μ CT scan files were used to reconstruct the three-dimensional surface of each molar crown through surface rendering, cropping, and smoothing. Figure 2A shows a visual representation of a paramyid mandibular molar in Amira, following surface rendering, cropping, and smoothing. Once these surface files were created for each tooth, they were then analyzed by the MorphoTester software (52), a Python-based application that is used for visualization and quantification of dental topography. Figure 2B shows a visualization of DNE for a paramyid mandibular molar in the MorphoTester software. This software provided DNE, RFI, and OPCR values for each specimen. These metrics have been used in several studies, including Boyer et al. (2008, 2009), Godfrey et al. (2012), Winchester et al. (2014), and Prufrock et al. (2016) to study the dietary niches of primates and rodents (11,19–21,53).

Figure 2. Paramyid mandibular molar after cropping, shown in (A) Amira and (B) MorphoTester. D=Distal, L=lingual, M=mesial, B=buccal.

A



Climate Data

Climate data from the late Paleocene- early Eocene of the Bighorn Basin was collected from Zachos et al. (2001). This study collected oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope data from bottom-dwelling deep-sea foraminifera. These data come from the literature and were compiled by Zachos et al. into one global deep-sea isotope record (43). $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ are used in this study as proxies for temperature and precipitation, respectively (43).

Statistical Analysis

All statistical analyses were performed using SPSS. Tests for the assumptions of equality of variance and normality were conducted. A Levene's test of homogeneity of variance indicated that the data met this assumption ($P=0.119$, 0.788 , and 0.578 for DNE, OPCR, and RFI respectively). However, a Shapiro-Wilk test showed that the data failed to meet the normality assumption for an ANOVA ($P<0.001$ for DNE, RFI, and OPCR), and thus a Kruskal-Wallis non-parametric test was utilized to examine dietary niche change over time for each separate dental topographic measurement, with the grouping variable of these analyses being the eight sub-NALMAs. To analyze all three dental topographic measurements together, a multivariate analysis of variation (MANOVA) was conducted, with the grouping variable being the eight sub-NALMAs. The MANOVA looked at the means of multiple dependent variables (the three dental topographic metrics) and assessed the hypothesis that dietary niche variation occurred across the sub-NALMAs, taking all three dental topographic metrics into account at once. This approach was chosen as each measurement captures a different aspect of dental topography, and previous research has demonstrated that the combination of these three measurements were potentially more successful in overall dietary prediction (19,24). The Kruskal-Wallis tests assessed the means of each dental topographic metric individually across the sub-NALMAs studied and determined if a significant difference existed among those means. Dunn's post hoc analysis was then conducted to compare dental topographic values from each time period to one another in instances where the Kruskal-Wallis test determined significant differences. This test identified any significant differences in dental topography (a proxy for dietary niche) between each pair of time periods.

Simple linear regression analysis was utilized to examine the association of dietary niche change with climate change. This analysis provides values to assess the strength of a relationship between two variables, dental topographic values and climate change in this study, and was conducted between each dental topographic variable and both deep sea oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope data from Zachos et al. (2001) for a total of 6 analyses. A multivariate regression was conducted to analyze the association between all three dental topographic measures in combination with each climate variable.

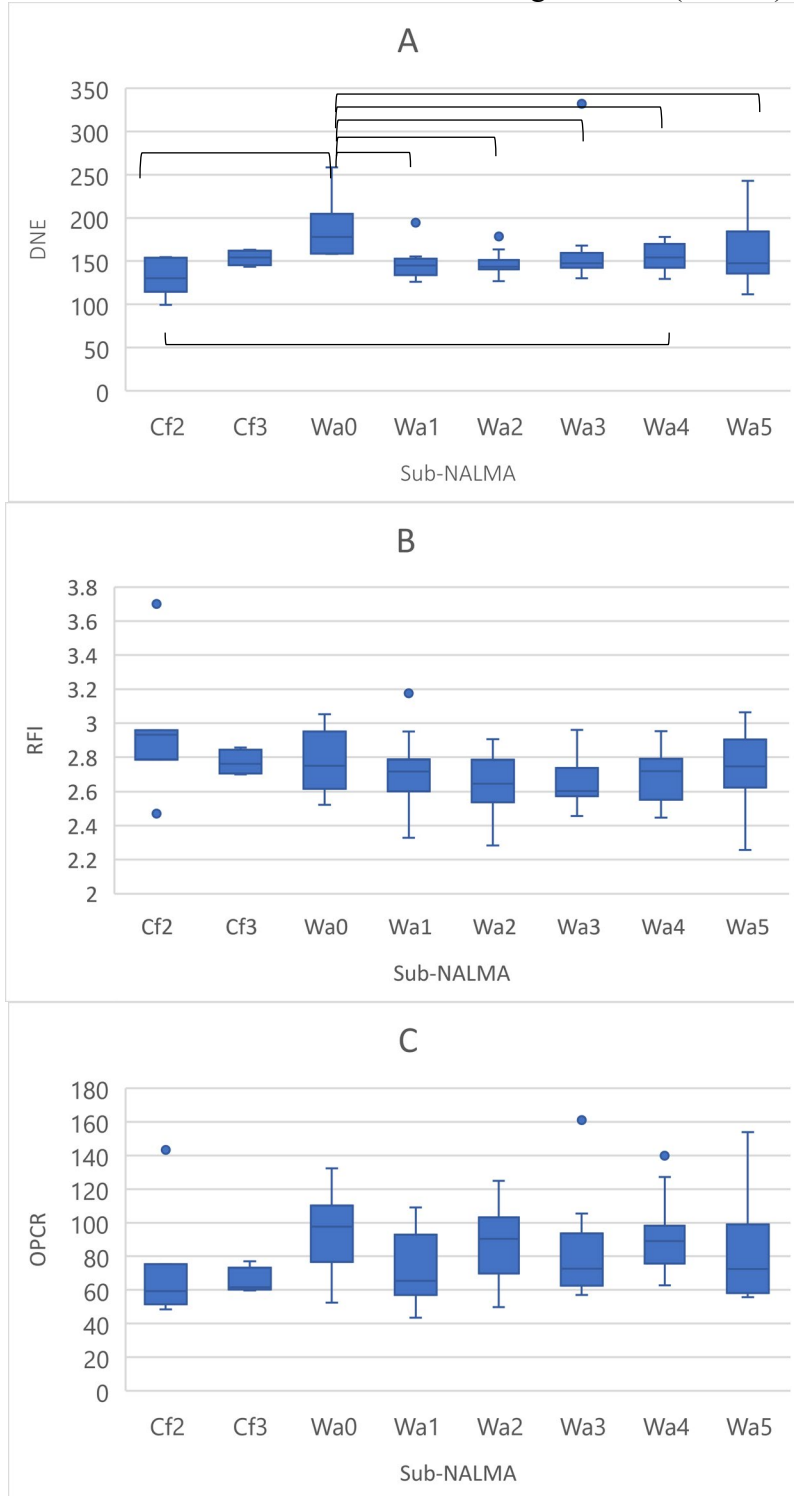
Results

Hypothesis 1

A Kruskal-Wallis test was conducted on each of the three dental topographic metrics to determine if any differences existed among the means of the metrics over the eight sub-NALMAs studied. DNE indicated a significant difference ($\chi^2 = 20.089$, $P=0.005$) between at least two sub-NALMAs. The results for OPCR and RFI, however, indicated no significant difference among sub-NALMAs ($\chi^2=13.367$, $P=0.064$, $\chi^2=12.087$, $P=0.098$). The means of each dental topographic measurement for each time period are illustrated in Figure 3.

In order to determine which sub-NALMAs were significantly different from each other, Dunn's post hoc analysis was carried out for DNE. This analysis indicated that there was a significant difference between the means of Cf2 and Wa4 ($P=0.037$), Cf2 and Wa0 ($P<0.001$), Wa0 and Wa1 ($P=0.000$), Wa0 and Wa2 ($P=0.001$), Wa0 and Wa3 ($P=0.011$), Wa0 and Wa4 ($P=0.023$), and Wa0 and Wa5 ($P=0.004$). These differences can be visualized in Figure 3A.

Figure 3. Boxplots for each of the dental topographic metrics over the eight sub-NALMAs. A=DNE, B=RFI, C=OPCR. Brackets indicate statistical significance ($P < 0.05$).



In addition to the separate Kruskal-Wallis tests performed for each dental topographic metric, a MANOVA was conducted to assess if there were differences in dental topography across the eight sub-NALMAs when considering the combination of DNE, RFI, and OPCR. This test determined a significant difference (Wilks' $\lambda=0.613$, $P=0.004$) among sub-NALMAs.

Hypothesis 2:

A simple linear regression analysis was conducted to determine if the observed changes in dietary niche over the sub-NALMAs studied had any association with known climate changes over the same time period. The assumption of absence of multicollinearity was met, with VIF values for each regression model below 10. Additionally, a Shapiro-Wilk test showed that the assumption of normally distributed data was met ($P=0.172$, 0.878 , and 0.162 for DNE, OPCR, and RFI, respectively). The regression analysis compared the means from each sub-NALMA for each dental topographic metric (DNE, OPCR, and RFI) to the means for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values, respectively, for each corresponding sub-NALMA (Tables 4,5). No significant associations were found between DNE, RFI, or OPCR and either of the climate variables. The multivariate plots in Figure 4 provide a visual representation for the dental topographic metrics and climate variables over the sub-NALMAs studied.

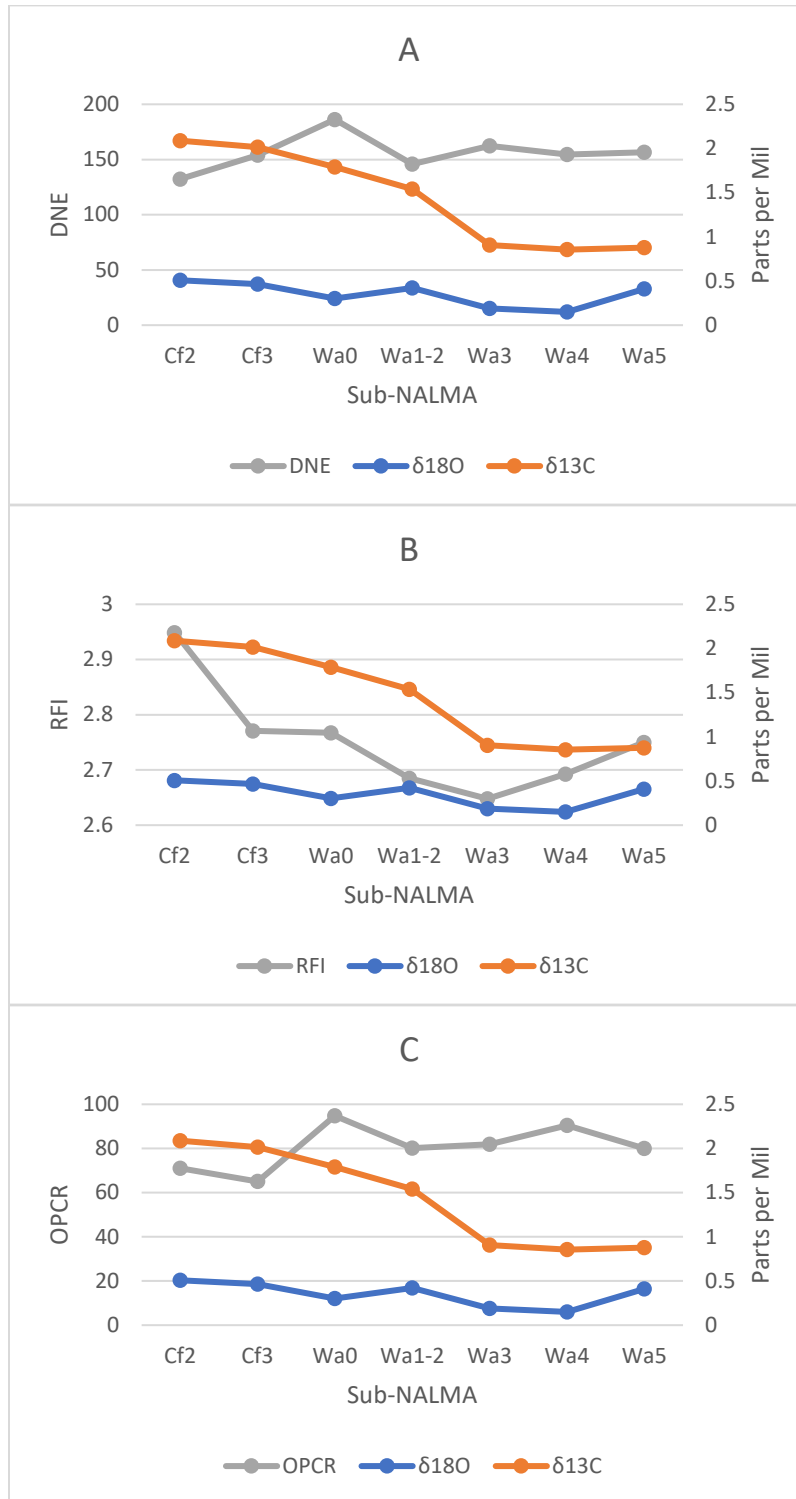
Table 4. Mean $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, DNE, RFI, and OPCR values for each sub-NALMA examined.

Sub-NALMA	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	DNE	RFI	OPCR
Cf2	0.508	2.088	132.338	2.949	71.054
Cf3	0.466	2.016	153.904	2.771	65.031
Wa0	0.303	1.790	186.235	2.768	94.781
Wa1-2	0.423	1.540	145.786	2.685	80.211
Wa3	0.189	0.905	154.249	2.648	76.403
Wa4	0.150	0.855	154.646	2.693	90.375
Wa5	0.409	0.876	156.631	2.750	79.979

Table 5. Simple linear regression results for each dental topographic metric and climate variable.

Dental Topographic Metric	Climate Variable	R ²	F-Value	P-Value
DNE	$\delta^{18}\text{O}$	0.170	1.023	0.358
	$\delta^{13}\text{C}$	0.011	0.055	0.824
RFI	$\delta^{18}\text{O}$	0.469	4.413	0.090
	$\delta^{13}\text{C}$	0.491	4.825	0.079
OPCR	$\delta^{18}\text{O}$	0.383	3.101	0.139
	$\delta^{13}\text{C}$	0.152	0.895	0.388

Figure 4. Multivariate plots of the dental topographic metrics and climate, with $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ serving as climate proxies. A=DNE, B=RFI, and C=OPCR.



To determine the association between the climate variables and all three dental topographic metrics together as a group, two multivariate regression analyses were performed with $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ as the independent variables, respectively. This analysis revealed no significant association between the dental topographic metrics and either $\delta^{13}\text{C}$ ($F=0.321$, $P=0.814$) or $\delta^{18}\text{O}$ ($F=0.590$, $P=0.678$).

Discussion

Previous research has demonstrated floral and faunal changes as a direct response to the PETM, beginning at the end of Cf3 and continuing into Wa0 (45). The associated ~5-6°C global temperature increase led to mammalian immigration into North America during Wa0 (42). This immigration is thought to have played a significant role in faunal dynamics during the Wa0 sub-NALMA, with further implications in later Wasatchian sub-NALMAs (45). The potential for these changes in faunal dynamics to have manifested in availability of, and competition for, resources (and thus ultimately play a role in changes to the dietary niche of the paramyids studied) formed the basis of the hypotheses for this research. Overall, this study does not fully support or reject the hypothesis that the dietary niche of paramyid rodents changed during late Paleocene-early Eocene (Hypothesis 1). Additionally, the results indicated that there is no association between dietary niche change and climate change during this time period, particularly across the PETM (Hypothesis 2).

One of the three of the dental topographic measurements utilized in this study supported Hypothesis 1, that dietary niche of paramyid rodents underwent change across the sub-NALMAs studied. Results indicated that DNE values were significantly different between Cf2 and Wa4, Cf2 and Wa0, as well as Wa0 and all other Wasatchian sub-NALMAs. As the PETM occurs across the end of Cf3 and into Wa0 (54), these results appear to support the idea that the large climate changes that occurred during the PETM led to significant changes in dental topography, and therefore dietary niche, during this time. DNE values displayed a significant increase from Cf2 to Wa0, and then displayed a significant decrease from Wa0 to all other Wasatchian sub-NALMAs. The DNE values indicate that, overall, the paramyid rodents studied possessed teeth with sharper cusps better suited for shearing across the end of the Clarkforkian. This suggests

that the paramyids at this time consumed a diet that was high in structural carbohydrates, like cellulose or chitin, which would be found a folivorous or insectivorous diet (11). DNE values then show a decrease across Wa0 to Wa1, with the mean of each of the subsequent Wasatchian sub-NALMAs remaining significantly lower than that of Wa0. This signifies that the teeth of paramyids after Wa0 had a lower curvature better suited for crushing food items. This decrease in curvature indicates that paramyids were likely relying less on tough structural carbohydrates for their diet and now possessed teeth that were more useful for crushing, an effective way to process food items such as nuts and berries in a frugivorous or granivorous diet. The remaining two dental topographic metrics used in this research, OPCR and RFI, contradicted the DNE results and did not indicate any significant changes in dental topography over the eight sub-NALMAs.

In order to assess any association of dietary niche variation with climate change, this research utilized deep-sea stable oxygen and carbon isotope records for bottom-dwelling, deep-sea foraminifera compiled by Zachos et al. (2001) (43). $\delta^{18}\text{O}$ data have been integral in the reconstruction of global and regional climate change, and are consistent with MAT data collected from fossil land plants, indicating a $\sim 5\text{-}6^\circ\text{C}$ temperature increase occurring at the boundary of the Paleocene and Eocene (ca. 55.8 Ma) (43). The $\delta^{13}\text{C}$ data indicates globally higher humidity and precipitation (43), supporting research that has indicated that the climate at this time was warm and wet (55). In using these isotope records as climate proxies, results of the regression analysis that assessed each dental topographic metric with temperature and precipitation variables determined that none of the dental topographic measurements showed an association between dietary niche variation and climate over the eight sub-NALMAs. It should be noted, however, that the p-value for linear regression analysis of RFI values and the $\delta^{13}\text{C}$ climate

variable does approach significance ($P=0.079$), though the R^2 value is low ($R^2=0.491$). When looking at Figure 4B, a downward trend can be seen for both RFI values and $\delta^{13}\text{C}$, specifically from Cf2 to Wa3. It is possible that, though the results do not indicate a significant association between RFI value and precipitation proxy values, when considering the small sample size of this study, a trend may exist.

The variation in results amongst the three dental topographic metrics for Hypothesis 1 is not unique to this study. Each dental topographic analysis assesses a different aspect of the tooth crown, with DNE focusing on curvature (22), RFI measuring the ratio of three-dimensional area to planar area (23), and OPCR considering the overall complexity of the occlusal surface of the molar tooth (11,21). As such, evaluating dental topographic metrics individually may lead to results that differ amongst themselves. This has been demonstrated in previous research (2,24), as not only do the measurements focus on different aspects of molar crown anatomy, but they also display varying levels of sensitivity to the potential human error involved in the cropping of the molar specimens (24).

In his research on primates with different dietary preferences, Bunn et al. (2011) observed discrepancies in the results obtained from different dental topographic measurements, concluding that of the measurements studied, which included all three used in this research on paramyids, DNE was the least sensitive to cropping and orientation, making it less vulnerable to data quality issues (24). Bunn et al. (2011) also employed a combination of analyses wherein multiple dental topographic metrics were combined to understand the capability of this combination of variables in predicting dietary niche, concluding that a combination of multiple dental topographic metrics was more effective in determining dietary niche than any individual analysis (24). A combination of dental topographic analyses was also utilized by Winchester et

al. (2014) and Pineda-Munoz et al. (2017) (2,19), with both studies supporting the same conclusions as Bunn et al. (2011). For this reason, this study applied this approach, evaluating a combination of all three dental topographic measures in addition to analyzing each measurement individually. The combination of the three measurements in this research supported the hypothesis that the paramyid dietary niche changed over the PETM and surrounding sub-NALMAs but rejected the hypothesis that this dietary niche change was directly correlated to climate change.

The reasoning behind the expectation of paramyid dietary niche change association with climate change in this research stemmed from the known mammalian immigration and changes in floral and faunal diversity that occurred over the PETM in the Bighorn Basin (40,45). These changes had the potential to disrupt the dietary niche utilized by paramyids before the onset of the PETM either through change in the availability of the paramyids' food resources or increased competition for those resources, as mammalian immigrants may have utilized the same dietary resources consumed by paramyids. The results of one of the dental topographic analyses and the analysis of the combined measurements do indicate some variation to the paramyid dietary niche among several of the sub-NALMAs studied, seemingly supporting the above reasoning. It should be noted that these paramyid rodents are thought to have been omnivorous (37), and as such would be considered generalists. Generalists rely on a wide range of food resources to make up their dietary niche (56). Additionally, generalists are well-suited to adapt to a changing environment, including the ability to adapt their dietary niche in the event of resource changes or competition (56,57). With a large variety of food resources to utilize (58), it is possible that observed changes in the paramyid dietary niche were the result of reliance on, or preference for, a different aspect of their broad dietary regime at different points across this time period.

Because the results of this study do not support an association between climate change and dietary niche change, it is not likely that dietary niche variation was a result of climate-induced competition, but rather occurred as a result of changes in availability of resources due to intermittent competition unrelated to climate change.

Literature on the changes to trophic structure of Bighorn Basin mammals at this time provides further evidence to suggest that these paramyid rodents did not experience an increase in competition for dietary resources over the sub-NALMAs studied as a result of climate change. As a time of mammalian community reorganization resulting in part from climate-induced immigration (42,45), the PETM displayed a rapid increase in species richness and evenness in the Bighorn Basin (42). In their studies of the mammalian response to the PETM in the Bighorn Basin, Clyde and Gingerich (1998) found that the mammalian immigrants generally had a larger body size with dietary niches that were mostly herbivorous and frugivorous as compared to endemic mammals (42). Analysis of the mammalian trophic structure during this time period indicates that the Clarkforkian was associated with a high abundance of omnivores and insectivores, while the Wasatchian was associated with greater abundances of herbivores, frugivores, and carnivores (42). The change in trophic structure of Bighorn Basin mammals at this time can be attributed to the aforementioned addition of mammalian immigrants whose dietary niche differed from that of the mammalian population prior to the PETM (42). As omnivores, paramyids may not have experienced strong competition for dietary resources as a result of these new mammalian immigrants, which could further explain the lack of association between dietary niche variation and climate change.

A challenge for this research stems from the extinct nature of these paramyid rodents and the inherent difficulty in collecting a large, viable sample of molars for evaluation. While μ CT

scans were taken of more than 93 paramyid first and second mandibular molars, there were several specimens with cracks, holes, or other issues that affected the integrity of the dental topography being studied. As a result, these specimens were removed from the sample and not analyzed. The overall sample size for this study was therefore relatively small, at 93 first and second mandibular molars. Additionally, the number of samples for each individual sub-NALMA was varied, with less specimens available for study in the older sub-NALMAs (Cf2-Wa0) than in the more recent sub-NALMAs (Wa1-Wa5). This variation in sample size, along with the overall small sample size, may have contributed to results that did not conclusively indicate whether climate change played a role in dietary niche variation of these paramyid rodents.

Though it appears that the paramyid dietary niche may have shifted across the PETM in the Bighorn Basin, the findings of this study indicate that this was likely not the result of this climatic event and the floral and faunal changes associated with it. An area of potential future study lies in the question of whether this significant climatic event impacted the dietary niches of other mammals in the Bighorn Basin. Several studies have looked at the overall impact of the PETM on mammalian faunal turnover (25,45) and on body size and trophic structure in the Bighorn Basin (42). While it is possible that paramyid rodents did not experience strong competition for resources as a result of the mammalian immigrants due to the breadth of their dietary niche and their ability to rely on a variety of resources to fulfill their dietary needs, mammals with frugivorous or herbivorous dietary niches prior to the PETM may have been affected differently by this event. These mammals would have been more likely to have experienced competition as a result of the influx of mammalian immigrants at the Paleocene-

Eocene boundary and could provide a further look at the effects of this large climatic event on the overall mammalian community from the Bighorn Basin.

Conclusion

This study found that the dietary niche of paramyid rodents did exhibit variation over the Paleocene-Eocene Thermal Maximum and the subsequent sub-NALMAs. However, this study did not find a close association between this dietary niche variation and climate change across the PETM. These results indicate that perhaps the dietary resources utilized by these rodents were unaffected by the climate changes that took place and did not experience climate-induced competition for dietary resources, or possibly that they were able to utilize other food resources available within their dietary niche classification.

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