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Tales in the Teeth: Using Isotopic Analysis to Understand the Paleoecology and Social Behavior of Brontotheres of the Intermountain Basins During the Middle Eocene

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TALES IN THE TEETH: USING ISOTOPIC ANALYSIS TO

UNDERSTAND THE PALEOECOLOGY AND SOCIAL

BEHAVIOR OF BRONTOTHERES OF

THE INTERMOUNTAIN

BASINS DURING THE

MIDDLE EOCENE

by

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of

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ABSTRACT

Tales in the Teeth: Using Isotopic Analysis to understand the paleoecology and social behavior of brontotheres of the Intermountain Basins during the Middle Eocene

by

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Utah State University, 2024

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Isotopic analysis has been a common practice used in paleontology to study ancient ecosystems, and the lives of animals therein. Oxygen isotopic analysis is of particular importance not only because of its use in studying paleoecology, diet, and migration, but also its use in studying mountain elevation, and its impact on ancient ecosystems. I use stable oxygen isotopic analysis to study the habits and ecology of brontotheres from intermountain basins surrounding the Uinta Mountains of Utah and Wyoming, USA. I studied the oxygen isotopes from 16 fossil specimens of teeth, most of which belonged to brontotheres, including the genera *Palaeosyops* and *Telmatherium*, with some complimentary material belonging to the extinct rhinoceros *Amynodon* and fossilized garfish scales from lacustrine sedimentary rocks. My results indicate a mild rain shadow resulting from the east-west trending Uinta Mountains during the Middle Eocene (48-46 Ma) that supported a range of habitats on either slope. The brontotheres appear to have exhibited different habitat preferences and lifestyles, with the smaller *Palaeosyops* favoring upland habitats as well as possibly being more semiaquatic compared to the larger *Telmatherium*, which was found in more lowland areas farther from the mountains. The isotopic data from *Amynodon* suggests a semiaquatic lifestyle, exhibiting a similar lifestyle to a modern hippopotamus. This data supports the use of oxygen isotopic analysis in studying the social behavior and ecology of extinct animals.

(47 pages)

PUBLIC ABSTRACT

Tales in the Teeth: Using Isotopic Analysis to understand the

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Intermountain Basin during the Middle Eocene

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Brontotheres are a family of rhinoceros-sized mammals from the Eocene (56-34 million years ago). Fossils have been found throughout Asia and North America, with many species living in the surrounding the Uinta Mountain Range. Using stable isotope analysis on fossil teeth discovered from depositional basins, in Utah and Wyoming, I examined oxygen isotopic values to answer questions about brontothere biology and ecology. I sought to investigate their sociability, lifestyle, and migratory behavior, as well as the kinds of habitats they lived in during the middle Eocene. I also investigated the biology and ecology of a contemporary large herbivore *Amynodon*, an extinct relative of the rhinoceros, to compare with brontotheres, with additional data from garfish scales serving as an isotopic comparison of their water drinking sources. These data can be used as a proxy to record the past elevation and environments surrounding the Uinta Mountains during the middle Eocene. Based on the data acquired from these isotopes, brontotheres inhabited different kinds of habitats, with the smaller *Palaeosyops* being more semiaquatic than the larger *Telmatherium*. *Amynodon* too appears to have been semiaquatic. The Uinta Mountains themselves appear to have supported a mild rain shadow that during the Eocene impacted the surrounding basins, but not severely enough for there to be major environmental differences between the two slopes of the mountain range during this period of time (48 to 46 million years ago).

Dedicated to my friends, from Wisconsin, Utah, and beyond, my loving family, and most of all my parents.

ACKNOWLEDGMENTS

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Chapter I: Introduction

Brontotheres are an extinct family of perissodactyls, or odd-toed ungulates, that lived during the Eocene epoch of the Cenozoic era. Although several different families of perissodactyls existed in Earth's history, only horses, rhinoceroses, and tapirs are extant. Brontotheres resemble rhinos in physical appearance and bulk but are more closely related to horses (Osborn, 1929). During the Eocene they were the largest land mammals on Earth, with *Megacerops coloradensis*, the largest North American species, measuring 2.5 meters in height at the shoulders, 4.63 meters in length, and weighing between 3.3 to 3.8 tons (Osborn, 1929). This is close in size to the extant African Forest Elephant, the third-largest living land animal.

Brontotheres are recognized by the horn-like ornamentations on the snouts of some species, a similarity to modern rhinos. Unlike rhinoceros horn, which is composed of keratin, brontothere horns have a bone core and are thought to have been covered in skin (Mihlbachler, 2005). The purpose of these horns is uncertain. Not all brontotheres possess these horns however, and so their most diagnostic synapomorphy is their tooth morphology. Unlike other perissodactyls, their upper molars have W-shaped ectolophs, or outer shearing blades (Gunnell and Yarborough, 2000). Alongside their short crowns, their design has been termed as bunoselenodont, a mix of cone (bunodont) and crescent (selenodont) patterns (Osborn, 1906). Based on their dental morphology and wear patterns, brontotheres are considered obligate browsers, eating primarily C3 vegetation, specifically leaves, shoots, and woody twigs (Zanazzi and Kohn, 2007; Boardman and Secord, 2013). Their dentition is best suited for shearing soft vegetation, not grasses or other gritty plants (Osborn, 1906). Low oxygen isotope ratios in their teeth suggests that some brontotheres

were very dependent on drinking water compared to other ungulates who may have fulfilled their water requirements from plants (Zanazzi and Kohn, 2007; Boardman and Secord, 2013; Table 7).

During the Eocene, brontotheres ranged across North America and Asia, with much of the known fossil record found in the surrounding basins of the Uinta Mountains of Utah, Colorado, and Wyoming (Gunnell and Yarborough, 2000; McCarroll et al, 1996). Known genera from this region include *Eotitanops*, *Palaeosyops*, *Telmatherium*, *Mesatirhinus*, and *Dolichorhinus* (Gunnell and Yarborough, 2000; McCarroll et al. 1996). Brontothere phylogeny is well studied (Mader, 1991; Mihlbachler, 2005; Mihlbachler, 2008), but many questions have yet to be answered about the behavior and ecological importance of these ungulates. For instance, was water dependency a common trait among brontotheres of the Uinta Mountains? What habitats did brontotheres prefer? Was habitat preference impacted by the topography and climate of the Uinta Mountains during the Eocene? Were brontotheres sociable or solitary mammals?

To answer these questions, I analyzed stable isotope ratios in the enamel fragments of brontothere teeth across a broad geographical region in the western United States. The primary focus will be on stable oxygen isotope ratios, which have played a key role in studying ancient climates, water cycles, and topography, as well as physiology of extinct animals. Research using oxygen isotopes has been used in paleoelevation of mountain ranges, a useful proxy for understanding ancient topography. While there is geological evidence for the uplift of the Uinta Mountains during the Eocene, there is debate on their paleo-elevation (Norris et al. 1996; Morrill and Koch, 2002). Conflicting studies used oxygen isotopes to suggest alternate hypotheses: either the mountains were so high that they could have been snowcapped and produced a rain shadow (Norris et al. 1996), or they were significantly lower in elevation and lacked a rain shadow (Morrill and Koch, 2002).

Here, I focus on the oxygen isotope ratios of at least two genera of brontotheres: *Palaeosyops* (Figure 1), and *Telmatherium* (Figure 2). These genera were studied because they had the most available described specimens. Several of the brontothere enamel fragments are indeterminate at a genus or species level. All enamel fragments assigned to brontotheres were found in strata from Utah and Wyoming dating back to the middle Eocene. Additionally, this research includes tooth fragments from the contemporary perissodactyl *Amynodon* (Figure 3) and fossil garfish ganoid scales from the extant genus *Lepisosteus* (Figure 4). *Amynodon* is the type genus of the family Amynodontidae, which are another group of perissodactyl ungulates that are considered proper members of the rhinoceros family (Bai et al. 2020). Much like brontotheres, their biology and ecology are not well studied, so the isotope ratios from the *Amynodon's* enamel can be compared with those of Middle Eocene brontotheres, in this case *Palaeosyops* and *Telmatherium*, to answer questions about both groups. The fossilized scales of garfish meanwhile can be used to compare with brontothere and *Amynodon* oxygen isotope ratios for paleobiological purposes. If it was semiaquatic like some other Amynodonts, I expect *Amynodon* oxygen isotopes to be far lower than those of terrestrial animals (Clementz and Koch, 2001). If the brontothere and *Amynodon* tooth values are like those of the garfish scales, it would indicate that these animals spent time in the water and may have been semiaquatic (Secord et al. 2008).

A major gap in our understanding about brontothere behavior is their sociability. Brontothere bonebeds, fossil sites that contain multiple individuals of a genus or species, are known, and have been suggested to represent groups of individuals that died together as a herd (Turnbull and Martill, 1988; Santos, 2018). But they are not common. Alternative methods could be used to test if other brontotheres were gregarious animals, and if so, the extent of their social groups. In modern mammals, oxygen isotope analysis has been used to study social behavior. For

example, in a 2009 study about migration in Alaskan Caribou, the oxygen isotope compositions of three individuals had very similar absolute values. Between four different locations, the values ranged from 13.2‰ ± 0.4 (1Δ) to 16.1‰ ± 0.3 (1Δ). This suggests they drank water from similar sources with the same isotopic values (Britton et al. 2009). Applied to brontotheres, if the values among individuals are similar to one another as seen in Caribou, it could be suggested that the studied brontotheres were part of a group or herd. If the values are significantly different from one another, then alternate interpretations should be taken into consideration about their social behavior.
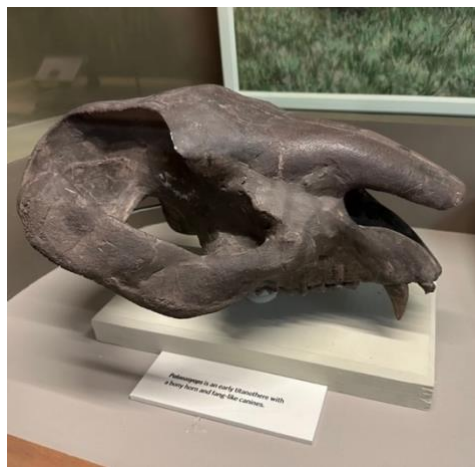
Figure 1: Skull of *Palaeosyops* at the University of Kansas' Natural History Museum.

Figure 2: *Telmatherium* material from 2023-TWI-22.

Figure 3: Skull of *Amynodon* at the University of Kansas' Natural History Museum.

Figure 4: Specimen Gar Scale 1 collected from the Green River Formation. The oxygen isotopes from these scales will be used for comparison with the tooth isotopes of my brontotheres.

Chapter II: Background

2.1 Summarizing Oxygen Isotopes and Fractionation

2.1.1 Oxygen Isotopes

Stable isotope analysis provides us with a mechanism to answer a variety of questions that cannot be answered by strictly looking at the bones themselves. In brief, an isotope is a variant of an element that has an equal number of protons but a different number of neutrons in their nuclei. This changes the atomic weight or mass number of the element, though the atomic number will remain the same. For example, there are three known stable oxygen isotopes: ^{16}O (8 protons, 8 neutrons), ^{17}O (8 protons, 9 neutrons), and ^{18}O (8 protons, 10 neutrons). ^{16}O is the most abundant of the three oxygen isotopes, representing 99.762% of all oxygen on Earth (Rosman and Taylor, 1999). This makes it the primary isotope of oxygen while ^{17}O and ^{18}O are secondary isotopes.

There are currently two international reference standards used to report variations in oxygen isotope ratios: Standard Mean Ocean Water (SMOW) and Vienna Pee Dee Belemnite (V-PDB). SMOW has a delta value of -29.99‰ (Brand et al. 2014), and in practice, a stretching factor of 0.8% is applied to oxygen isotope analyses using SMOW (Sharp, 2017). The stretching factor serves as an offset correction, which is necessary when converting between SMOW and V-PDB standards. This helps make the results of the analyses more comparable. V-PDB is restricted to analyses of oxygen isotope compositions of carbonates originating from oceanic, lacustrine, and pedogenic depositional environments (Sharp, 2017). Often V-PDB is used in studies on paleoclimate, paleoceanography, and carbonate diagenesis (Clarke and Jenkyns, 1999; Ravelo and Hillaire-Marcel, 2007; Swart, 2015).

2.1.2 Fractionation

To properly analyze stable isotopes in oxygen, scientists must understand fractionation, a separation mechanism whereby processes change the relative proportions of various isotopic compositions. There are two major causes of fractionation in isotopes: kinetic and equilibrium processes. Kinetic processes separate stable isotopes in a single, unaltered sequence (Kendall and Caldwell, 1998). These processes can include evaporation of water into the atmosphere as well as diffusion of energy from a region of higher concentration to a region of lower concentration (Sharp, 2017). During evaporation, the transition from liquid water to a gas is unidirectional, with water molecules with isotopically lighter compositions (such as ^{16}O) evaporating more easily than those with heavier compositions (such as ^{18}O). Consequently, the atmosphere becomes enriched in ^{16}O, while the original source, such as a lake or an ocean, becomes enriched in the heavier isotopic composition ^{18}O. This separation is further assisted by the lighter isotopes' lower disassociation energies, making their bonds weaker (Sharp, 2017). Because of the nature of the process, whereby the separation is absolute, kinetic fractionation is irreversible (Sharp, 2017).

Equilibrium processes are, by contrast, partial separations of isotopes, which make them reversible (Sharp, 2017). Reductions in vibrational energy when larger isotopes are replaced by lighter ones are the cause for most equilibrium fractionations (Maggi and Riley, 2010). The concentrations of the larger isotopes increase based on the location of high forces between chemical bonds, as these are most sensitive to replacement of isotopes (Maggi and Riley, 2010). An example of an equilibrium fractionation can be seen in condensation. As water vapor molecules come together and liquid water forms, heavier isotopes ($H_2{}^{18}O$) enrich the liquid while the vapor is more enriched by lighter isotopes ($H_2{}^{16}O$) (Kendall and Caldwell, 1998). Equilibrium

fractionations are best used in low temperature settings and serve as one of the bases for

paleoclimatology research, widely used as climate proxies (Urey, 1947). This ties them with the

typical depositional environments that are studied under the PDB standard, as the restricted habitats

are low-temperature origin sources by nature (Sharp, 2017).

2.2 Oxygen Isotopic Analysis in Modern Animal Metabolism and Paleontology

Isotopic analyses identify signatures of the abundance of certain isotopes within both

organic and inorganic compounds. They are used in a wide variety of natural science disciplines,

namely archaeology, ecology, hydrology, and geology. Typically, geologic analyses focus on

isotopes in conventional rocks, but research in the last several decades have helped expand this to

more specific fields, such as paleontology. In the 1970s, Italian geochemist Antonio Longinelli

suggested that oxygen isotopic analysis could be conducted on fossil bones and teeth to better

understand the biology and ecology of extinct animals (Longinelli, 1973). He reasoned that the

ratios acquired from fossils could determine meteoric (drinking) water values in ancient terrestrial

ecosystems. These values are the result of factors such as temperature, latitude, and altitude. $\Delta^{18}O$

values decrease with increasing latitude as temperatures decrease (Meehan et al. 2004). Similarly,

increasing altitude leads to lighter isotope compositions in water due to cooler temperatures

(Meehan et al. 2004). All these factors can serve as a proxy for paleoclimates among other aspects

of the prehistoric world. This, in theory, could answer questions about extinct animals that

otherwise could not be ascertained from simply observing the bones (Longinelli, 1973).

The basic idea behind this hypothesis is that oxygen isotopes, specifically the ^{18}O variety,

have bone and tooth apatite values that result from the ^{18}O values in an animal's body water. The

body water values are determined based on the drinking water an animal ingests. From this the phosphate minerals that reside in tooth apatite can serve as a proxy for ancient meteoric water values, and by extension paleoclimates (Longinelli, 1973). To put this into perspective for this study, teeth are made up of four chief components: enamel, cementum, pulp, and dentin. Dentin is usually covered by enamel on the crown, and is chemically made up by 22% water, 33% organic material, and 45% hydroxyapatite (HA) (Ten Cate and Nanci, 2013). HA is a form of calcium apatite that makes up 50% of the volume and 70% of the weight in human bones. It is from this mineral that scientists can determine values of tooth apatite (Singh et al. 2018).

Longinelli primarily focused on fossil mammals for this analysis because mammals are typically homeotherms (Longinelli, 1984). This means that they maintain a constant internal body temperature regardless of external influence from the surrounding environment or physical activity. Because body temperature can influence the ^{18}O values found in teeth, its stability within an organism can be vital in acquiring reliable data. Longinelli's criteria for this research also relied on the oxygen isotope composition being principally driven by the composition seen in drinking water, and that the oxygen isotopes of the phosphate in bones and teeth are equal to the animal's body water (Longinelli, 1984). First testing this hypothesis using modern mammals, specifically domestic pigs, deer, wild boar, and humans, Longinelli found that the ^{18}O values between blood and bone were constant (Longinelli, 1984).

Scientists expanded upon Longinelli's initial hypothesis by creating a quantitative explanation for the relationship between ^{18}O values seen in body water and drinking water (Luz et al. 1984). Organisms acquire these values by drinking water, intaking oxygen from the atmosphere, and consuming oxygen that remains in plant material or meat. The ^{18}O values in atmospheric oxygen is constant across the Earth, but vary considerably in surface water and food,

both of which are related to the values seen in local meteoric water (Luz et al. 1984). ^{18}O values can also exit an organism via urination and sweating, water vapor in one's breath, and the exhaling of CO_2. During exhalation, we dispel some amount of excess oxygen that ends up not being used by our respiratory system alongside the naturally produced CO_2 (Luz et al. 1984).

In mammals, both the intake and output of oxygen are equal in an animal whose size remains proportional to its individual ^{18}O values (Luz et al. 1984). Similar proportionality can be seen when taking body size into account. In species that weigh 1 kilogram or more, there is an exponential increase in the amount of water ingested (Nagy and Peterson, 1988; Bryant and Froelich, 1995). This is based on a model that predicts that the ^{18}O in a creature's body water is greater than in the water it drinks. Metabolism and body size are also proportional, with an animal's basal metabolic rate increasing with overall mass (White and Seymour, 2003).

Any deviation in the ingestion or excretion of oxygen will alter the ^{18}O values within an organism. An example of this is an animal's metabolic rate. Compared to body size, the relationship between metabolism and the amount of water an animal ingests is disproportional. The greater the metabolism, the less an animal drinks, and therefore the less proportional the relationship between internal body water and external drinking water is (Luz, 1984). Modern small herbivorous animals fulfill most of their water requirements from the food they eat, not from surface water. Plants themselves have varying ^{18}O values due to evaporative water loss as a function of humidity, which can alter the ^{18}O values seen in a herbivore's teeth (Luz, 1984). Digestion can also play a factor in the water dependency of herbivores. Ruminant artiodactyls, odd-toed ungulates with four-chambered stomachs, are less water dependent compared to non-ruminant artiodactyls and perissodactyls (Zanazzi and Kohn, 2008).

The principles discussed in this report are invaluable to gauge water dependency in modern animals, which can help explain aspects of their diets, behavior, and habitats. It is therefore not unreasonable to use these same techniques in the study of extinct organisms. In fact, previous studies have used stable oxygen isotopic analysis to better understand the behavior and paleoecology of extinct animals. For example, in Early Eocene fossils from the Willwood Formation of Wyoming's Bighorn Basin, oxygen isotope ratios in fossil mammal teeth have been used to interpret a wet, humid environment based on the narrow range of ^{18}O values in the sampled species (Secord et al. 2008). High ^{18}O values in the primate genus *Cantius* suggest that it acquired water from an evaporated source, such as fruit, rather than actual bodies of water. Meanwhile, significantly lower ^{18}O values found in the dentition of the large pantodont *Coryphodon* suggest that it was semiaquatic in nature rather than fully terrestrial (Secord et al. 2008). This is because semiaquatic behavior reduces aerial evaporative transpiration, which typically enriches body water with ^{18}O (Kohn, 1996). Elevated water turnovers and water loss in semiaquatic animals also contributes to these lower values (Bentley and Schmidt-Nielsen, 1965).

2.3 Brontotheres of the Uinta Mountains

The Uinta Mountains are a subrange of the Rocky Mountains that trend in an east-west chain along northeastern Utah before slightly extending into northwest Colorado and southwest Wyoming. The oldest rocks of the Uinta Mountains date back between 700 and 760 million years during the Neoproterozoic age, but the actual uplift itself is much more recent (Dehler et al. 2010). Building of the Uintas began during the Laramide orogeny from 70 to 50 million years ago, from the late Cretaceous period to the early Eocene epoch (Hamilton, 1981). Today their highest point,

Kings' Peak, stands at 4,123 meters (13,528 feet), but the elevation of the Uintas during the Eocene has been the subject of debate. Stable isotopic analysis of oxygen has been used to argue conflicting interpretations of the range's elevation. For example, measurements of isotopic compositions of microbial carbonates from Lake Gosiute in Wyoming suggested that negative estimates of $\Delta^{18}O$ values were the result of snow melt ^{16}O being mixed with that of annual rainfall. Therefore, the mountains would have to be high enough to support snow caps that would produce meltwater (Norris et al. 1996).

Conversely, the low $\Delta^{18}O$ values of microbial carbonates could be due to diagenetic overprinting, where earlier mineralogical characteristics are obscured by more recent ones. Analysis of fossil bivalves (clams and their relatives) from the region showed that $\Delta^{18}O$ values in their shells were far higher than what would be expected for water bodies receiving meltwater from mountains. Evidence for seasonal meltwater plumes entering lakes like Gosiute may reconcile this discrepancy, but no such indicators have been found in low $\Delta^{18}O$ values. Instead, low $\Delta^{16}O$ values appear in bivalve samples that were altered by overprinting (Morrill and Koch, 2002). The evidence in this case leans closer to continental precipitation, and the cycles in ^{18}O could be explained though conventional changes in seasonality rather than snowmelt. The conclusion therefore is that the Uintas did not have especially high elevations (Morrill and Koch, 2002). Because mountains can play an important role in shaping habitats and the ecological communities therein, studying the oxygen ratios between geographically widespread areas is crucial to understanding how the Uintas impacted the lives and habitats of Eocene mammals, such as brontotheres.

Brontotheres lived throughout the entire Eocene epoch, originating in the Ypresian stage, which began 55.8 million years ago (Steurbaut, 2006), and dying out in the Priabonian stage,

which ended about 33.7 million years ago (Odin et al. 1991). This chronology is based on the
International Commission on Stratigraphy's time scale, which is used to understand global
stratigraphical, geological, and geochronological discoveries. In addition to this global system,
every continent, except Antarctica and Australia, has their own individual geologic classifications
based on their unique faunas and zoological turnovers within mammal paleontology (Wood et al.
1941). These are known as Land Mammal Ages. As the brontotheres used in this study come
exclusively from North America, this report will use the North American Land Mammal Age
chronology, from here on referred to as NALMA. This system will help correlate specific
occurrences within North America itself, specifically within the western United States, for this
study.

Using the NALMA chronology, my brontothere specimens date back from the Bridgerian
NALMA, which began about 50.5 million years ago (Clyde et al. 1997), to the Uintan NALMA,
which ended at about 40 million years ago (Townsend et al. 2006). The specimens used for this
study were found in the Uinta and Green River Formations of Utah, and the Washakie and Bridger
Formations of Wyoming, and are all dated between 48.27 and 46.46 million years ago (Murphey
et al. 2017). This is based on Argon 40 and Argon 39 dating of ash layers in both Wyoming and
Utah (Murphey et al. 2017), the region all specimens were collected from or were adjacent.

The Washakie Formation is dated from the late Bridgerian to the early Uintan NALMAs
(Tomiya et al, 2021). Brontotheres from the Washakie Formation include *Dolichorhinus*,
Mesatirhinus, *Metarhinus*, and *Telmatherium* (McCarroll, Flynn, and Turnbull, 1996). The Bridger
Formation also spans the Bridgerian to Uintan NALMAs (Lewis Gazin, 1976). It has produced
material for *Telmatherium* and *Mesatirhinus*, as well as *Eotitanops* and *Palaeosyops* (Gunnel and
Yarborough, 2000; Figure 5). Ganoid scales of the garfish *Lepisosteus* are known from the Bridger

and Green River Formations (Figure 5). The Uinta Formation meanwhile is exclusively from the Uintan NALMA. Like the Washakie and Bridger, it has produced *Metarhinus*, but also has the later genera *Diplacodon* and *Protitanotherium* (Prothero and Emry, 1996). *Amynodon* appears at the beginning of the Uintan NALMA within the Washakie and Uintan Formations (McCarroll et al. 1996; Prothero and Emry, 1996; Figure 5).

Although several the specimens used in the study are of indeterminate genus or species, one has been assigned to a species of *Palaeosyops* and three to *Telmatherium validus*. The results of this report could provide insight into the lives and habits of at least two members of the family. Of the twenty-three specimens used in this report, ten of these were brontothere and amynodont enamel specimens originally held at the Utah Field House of Natural History State Park Museum in Vernal, Utah, while twelve more enamel fragments, all from indeterminate brontotheres, were collected from the Washakie Formation. The indeterminate gar scale previously mentioned in the introduction was collected several miles southwest of Duchesne, Utah. (fairly complete jaw/sometimes fragments of teeth make it difficult to identify)

2.4 Paleoenvironmental Settings

Each of the formations in this report displays paleoenvironmental settings that are roughly similar, but individually distinct. Understanding these ancient habitats will shed light on the environments the animals in this study lived in, and if the elevation of the Uinta Mountains impacted them. Research into the Green River Formation suggest a humid, subtropical to warm temperate climate, with a mean annual temperature of 55°F (Murphey et al. 2017). Trees of palm,

cinnamon, maple, and hazel, as well as cattails and rushes, are among the plant fossils discovered in the formation (Murphey et al. 2017).

The Washakie Formation is not as rich in fossil flora as the Green River Formation. Geographically adjacent to the Washakie, plant macrofossil assemblages come from lacustrine deposits that have been interpreted to represent a mixed deciduous and evergreen woodlands under a seasonally dry to tropical climate (Tomiya et al. 2021).

The Bridger Formation has recognized fluvial, lacustrine, mudflat, and volcanic depositional environments that support an interpretation of groundwater fed lakes and ponds (Murphey et al. 2017). Although the Bridger is divided into four distinct geologic sections, the general interpretation of the formation is of a woodland or forest habitat (Townsend, 2004). The abundance of primate, turtle, and crocodilian fossils from the formation support a tropical or subtropical climate (Townsend, 2004).

The Uinta Formation's depositional environments are described as river channels, floodplains, and river deltas that supported riparian forests amid a predominantly savanna type habitat with intermittent marshes, swamps, and forested highlands (Murphey et al, 2017). This is a significant deviation from the other formations in this report and has been attributed to a shift to a drier, more arid climate. This has been associated with the transition from the Bridgerian NALMA into the Uintan NALMA (Murphey et al, 2017), although other studies argue that this transition is independent of the change in NALMAs (Townsend, 2004). In either scenario, the shift seems to be independent of the Uinta Mountains and their elevation. Nevertheless, the Uinta Formation's distinct paleoenvironment is important to distinguish should this explain the biology and ecology of brontotheres from the area.
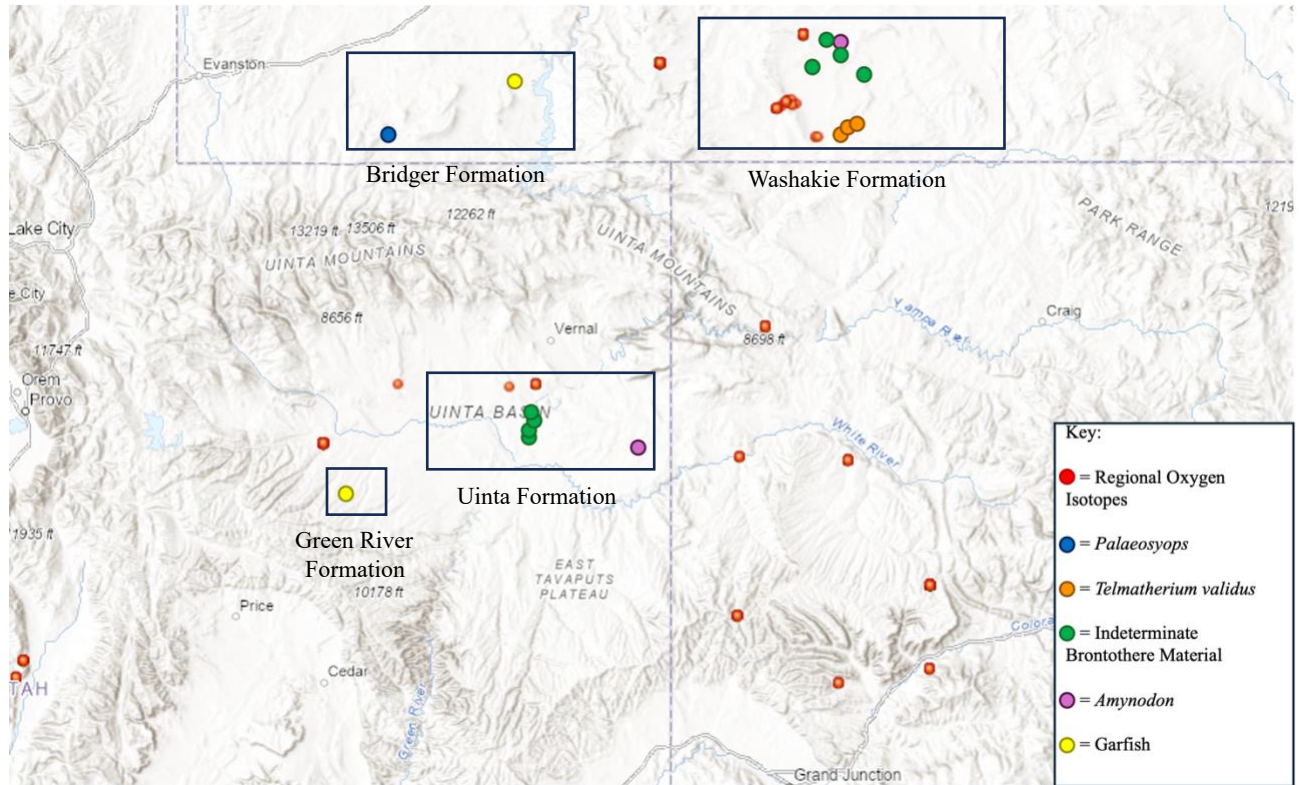
Figure 5: Map of the Uinta Mountains with sites indicating locations where specimens were discovered. Studied formations are labelled and identified. Regional carbonate isotopes from the PATCH Lab (2024) are shown for comparison with fossil values.

2.5 Purpose of Study

It cannot be understated the importance of oxygen isotopes in the study of extinct organisms. While bones themselves can determine an animal's appearance, size, locomotion, diet, and biomechanics, they are limited in answering more complex questions about the kinds of niches an animal took up in its natural habitat, their dependency on water, and other aspects of their lives. Isotopes overall can help answer these questions. With regards to brontotheres of the Uinta mountains, oxygen isotopes can shed invaluable light into the biology and ecology of these herbivores. As mentioned previously, much of the research that has gone into this family of

ungulates focuses on their systematics and phylogenetics whilst publications about their habitats and behavior are scarce. This study aims to explore the lives of the brontotheres from the Uinta Mountains, and answer important questions about their sociability, potential migratory behavior, or lack thereof, and the kinds of habitats they inhabited back during the Eocene epoch.

Chapter III: Materials and Methodology

3.1 Specimen Acquisition

Two series of fossils were selected from the collections of the Utah Field House of Natural History Museum for destructive analysis. They were chosen because they were scales and fragments of enamel, with little display value to the museum, and permission was easily granted for destructive analysis. Some of the fragments were associated with complete jaws while others were isolated and therefore indeterminate. As such none of the analysis involved the destruction of whole teeth. Past studies have done destructive analysis on specimens less than five milligrams in size with successful results, making data collecting more efficient than by destroying whole specimens. Acquiring these specimens meant receiving permission from their original owners, specifically the state of Utah and the Bureau of Land Management (BLM). With assistance from my advisor, Dr. Benjamin Burger, I used specimens collected under permit PA13-WY-205, as well as specimens in the museum collections previously excavated. Permission was sought from Utah's State Paleontologist Dr. James Kirkland, Dr. Brian Breithaupt, Wyoming's regional BLM paleontologist, and Katie Orr, Branch Chief for Outdoor and Heritage Resources for Utah's federal lands. Each reviewed my request to use destructive analysis on the specimens, as well as Dr. Burger's letter of recommendation, and approved of the study, including the destructive

analysis of these specimens. In total, I used 16 specimens: two for *Amynodon*, three for

Telmatherium, one to *Palaeosyops*, eight for indeterminate brontothere enamel fragments, and two

for garfish (Table 1). The Bridger Formation specimens come from the Bridger D and Bridger E

beds of the Twin Buttes Member, the Washakie Formation specimens are from the Lower and

Adobe Town Members, and the Uinta Formation fossils are from the Uinta C member. In

correlation of the biostratigraphy and available radiometric dates, there is a suggested time frame

of 1-1.5 million years in duration, spanning both the late Bridgerian and early Uintan NALMAs

(Murphey et al, 2017).

In compilation with past research on brontotheres, Eocene paleoenvironments, and oxygen

isotopic analysis, I make several predictions as to what the results may reveal about these

ungulates. If the oxygen isotope values are as low or lower than the values of species in prior

research, then these brontotheres would have also been very dependent on drinking water. If their

values are like those of the garfish specimens, it would suggest they were more semiaquatic rather

than fully terrestrial animals. If the brontotheres show little variance in their oxygen isotope

values, it would suggest that the individuals in this study may have been members of the same

herd. If the variance is significant, alternate social groupings may need to be considered.

I also make predictions about the topography of the Uinta Mountains during the Eocene

using my isotope values. This is based on the east-west positioning of the mountain range, and

what the environments would have been like on either the northern or southern slopes of the

Uintas. If the mountains had a high elevation and were snow capped, the values of the brontothere

isotopes from the north slopes of the Uinta Mountains would be significantly less than those

collected from the southern slope. This would indicate that the Uintas supported a significant rain

shadow effect. If the mountains were lower, the values of the two sets of brontothere teeth would

be more alike one another. A rain shadow could still be interpreted in this scenario, but it would be

milder and more comparable to rain shadows in mountain ranges such as the Apennines in Italy

(Giustini et al. 2016). Today, on the north slope of the Uinta Mountains in Henry's Fork, oxygen

isotopes have been recorded as being -17.002783, and on the south slope in the Duchesne River

being -15.690752 with a difference of 1.312 (Bowen et al. 2011).

Table 1: Complete list of specimens.

Catalogue or Locality #	Identification	Formation	State	Land Ownership	Latitude	Longitude
12762	*Amynodon* sp.	Uinta	Utah	BLM	40.092367	-109.175690
18436	*Amynodon* sp.	Washakie	Wyoming	BLM	41.407500	-108.226111
11023	Brontothere indet.	Uinta	Utah	State	40.132872	-109.612167
11031	Brontothere indet.	Uinta	Utah	State	40.171512	-109.611451
11032	Brontothere indet.	Uinta	Utah	State	40.171822	-109.610258
11299	Brontothere indet.	Uinta	Utah	State	40.170511	-109.611365
12335	Brontothere indet.	Washakie	Wyoming	BLM	41.358596	-108.345457
12349	Brontothere indet.	Washakie	Wyoming	BLM	41.392621	-108.233825
13975	Brontothere indet.	Washakie	Wyoming	BLM	41.294938	-108.108453
18439	Brontothere indet.	Washakie	Wyoming	BLM	41.438055	-108.268333
2023-TBR-08	*Lepisosteus*	Bridger	Wyoming	BLM	41.21419	-109.66076
Gar Scale 1	*Lepisosteus*	Green River	Utah	BLM	39.99842	-110.34760
2021-TBR-01	*Palaeosyops* sp.	Bridger	Wyoming	BLM	41.094444	-110.182500
2023-TWl-17	*Telmatherium validus*	Lower Washakie	Wyoming	BLM	41.10550	-108.14300
2023-TWl-22	*Telmatherium validus*	Lower Washakie	Wyoming	BLM	41.10652	-108.14050
2023-TWl-23	*Telmatherium validus*	Lower Washakie	Wyoming	BLM	41.09661	-108.15221

3.2 Sample Preparation and Isotope Analysis

Each of the enamel fragments was ground up into a fine powder. Specimens 2021 TBR-01, 12335, 12349, and 18439 were evenly split into two groups; samples treated with acetic acid and those untreated. Acetic acid reacts to calcite ($CaCO_3$) and dissolves it from the specimen. This reduces the risk of diagenetic calcite infiltrating a specimen via ground water interfering with the isotope values. Using coffee filter paper, specimens were left to dry after their acid treatment for four hours. Afterwards the powdered fossil specimens were placed in glass beakers and taken to Utah State University's Logan campus for stable isotopic analysis.

Upon being weighed for analysis, the specimens were placed in a sealed test tube and treated with phosphoric acid for twelve hours. The acid reacts to the HA in the teeth to liberate the oxygen from bondage with gaseous CO_2 inside the test tube. The released CO_2 builds up in the test tube, which upon puncturing with an auto-sampler is evacuated in a currier gas of helium and measured. The primary measuring instrument used was a Thermo Scientific Delta V Advantage isotope ratio mass spectrometer (IRMS). The IRMS is coupled to three peripheral devices to assist in measuring stable isotopes: a Thermo Scientific Gasbench II, a Thermo Scientific TC/EA with zero-blank autosampler, and a Costech 4010 Elemental Analyzer with zero-blank autosampler. The atomic mass of each CO_2 molecule is measured by the mass spectrometer, yielding oxygen and carbon isotopic values (Table 2). Multiple aliquots were collected from each powdered tooth sample and analyzed separately for carbon and oxygen isotopes (Table 3).

3.3 Mineralogy of fossil brontothere teeth

Oxygen isotopes in fossils, especially fossil teeth, run the risk of being altered by the infiltration of ground water during the process of fossilization. This usually occurs during permineralization of calcite ($CaCO_3$) which can contaminate results of oxygen isotopes to diagenetic factors (Koch et al. 1997). To account for this, another tooth belonging to my *Palaeosyops* specimen was saved for mineralogical analysis (Figure 6). This was done to study the preservation of the tooth and ensure that the $\Delta^{18}O$ values were not altered during the fossilization process due to diagenetic $CaCO_3$. Analysis was carried out by taking thin sections of the tooth root that could be viewed from under a microscope. Notably, part of the dentary was connected to the tooth, meaning that the thin section displayed the mineralogy of the lower jawbone as well as the molar's mineralogy. To accomplish this, the tooth was placed in a polymer resin cast that would protect the tooth from complete destruction of the specimen. After being split into two halves, each side with the tooth facing upwards was flattened, allowing for a glass pane to be secured onto the bone. Once the pane was fastened, the thin section was safely removed with no further damage to the tooth itself, providing a sample with a thickness of 30 μm.

After the thin sections were made, further analysis could commence under a microscope, whereby individual elements could be identified, including microscopic bone fragments and $CaCO_3$. Taken from under a microscope, the images of the thin sections of 2021-TBR-01 revealed that the tooth enamel contained little if any diagenetic $CaCO_3$ (Figure 7). The dentary bone that was still attached to the tooth (Figure 6) was fossilized through permineralization of $CaCO_3$ that filled in some of the bone cavities. However, the enamel appeared darkly stained containing the original organic material from the living animal, including oxygen which was mineralized when the *Palaeosyops* was alive. The darkness of the enamel is caused by organic carbon molecules

because of bioapatite. The brightly colored minerals meanwhile represent new minerals that

replaced and then fossilized the surrounding bone, showing the petrographic properties of $CaCO_3$.

Figure 6: Tooth from *Palaeosyops* used for mineralogical analysis.

3.4 Statistical Analysis

I also conducted two statistical tests of my results. The first was a population variance test to gauge the level of statistical variance between specimens and species, which I can then use to interpret whether the brontothere specimens represent members of a single herd, were solitary, or were members of multiple groups (Table 4). The second was a T-test that compared the variance between the northern and southern brontothere specimens, giving us a way to gauge variation between brontotheres on either side of the Uinta Mountains (Table 5) (add throw away sentence in methods lol). By doing so we can see if there was a stark difference in total isotope values between the northern and southern Uintas.
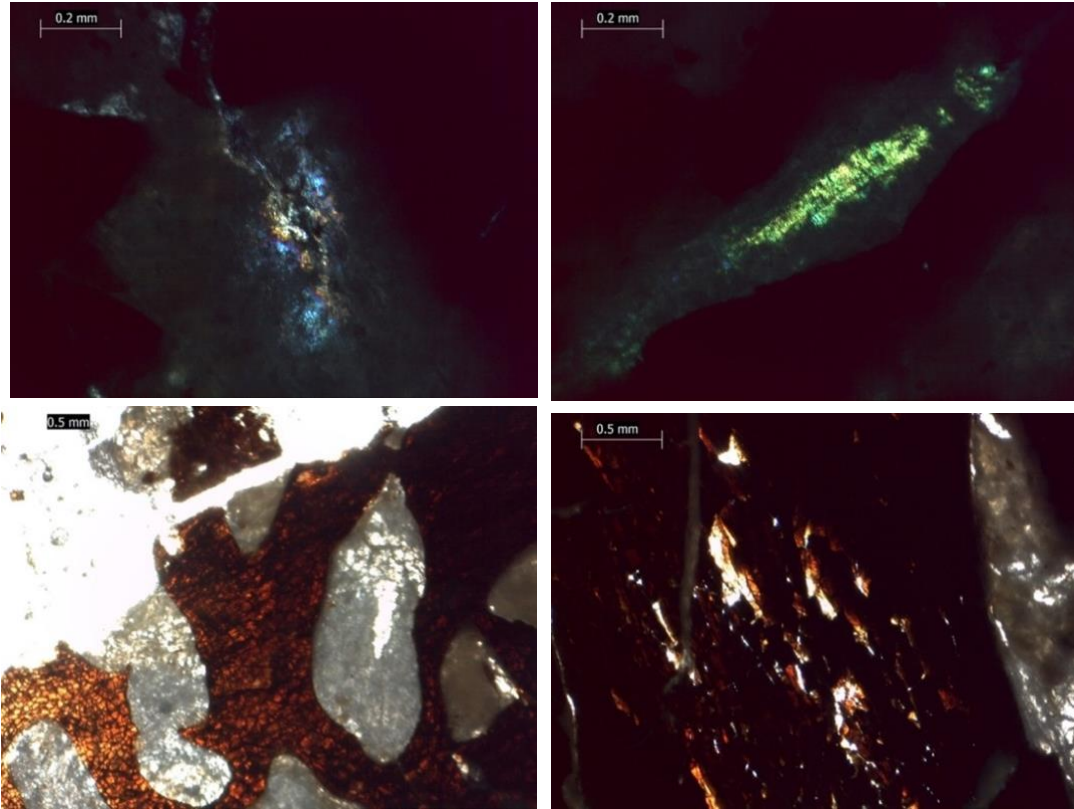
Figure 7: Four pictures taken from thin sections of my *Palaeosyops* specimen under a microscope. Two were taken under regular polar light (top left; top right), while two were taken under cross polar light (bottom left; bottom right). The bottom left image contains bits of bone that are rich in $CaCO_3$. The bone is dark orange to black in color while the CaCO3 is a bright white. Under cross polar lighting, the CaCO3 is bright blue or green in color.

Chapter IV: Results

Using the SMOW standard, the resulting oxygen isotope values range between 13 and 22‰ SMOW (Table 2). The lowest ^{18}O values were found in the *Lepisosteus* and indeterminate gar scale material. Individually, *Palaeosyops* had the lowest values of all the studied brontotheres (Figure 9). Several of the indeterminate brontotheres have higher isotope values than either *Palaeosyops* or *Telmatherium* (Figure 9).

Table 2: Complete list of specimens with $\Delta^{18}O$ values following analysis.

Catalogue or Locality #	Identification	Formation	State	NALMA	Latitude	Longitude	$\Delta^{18}O$ (‰ SMOW)
12762	*Amynodon* sp.	Uinta	Utah	Uintan	40.092367	-109.175690	16.90
18436	*Amynodon* sp.	Washakie	Wyoming	Uintan	41.407500	-108.226111	17.85
11023	Brontothere indet.	Uinta	Utah	Uintan	40.132872	-109.612167	18.73 ±0.42
11031	Brontothere indet.	Uinta	Utah	Uintan	40.171512	-109.611451	21.91
11032	Brontothere indet.	Uinta	Utah	Uintan	40.171822	-109.610258	20.58
11299	Brontothere indet.	Uinta	Utah	Uintan	40.170511	-109.611365	20.64 ±0.08
12335	Brontothere indet.	Washakie	Wyoming	Uintan	41.358596	-108.345457	21.04 ±0.38
12349	Brontothere indet.	Washakie	Wyoming	Uintan	41.392621	-108.233825	21.13 ±0.4
13975	Brontothere indet.	Washakie	Wyoming	Uintan	41.294938	-108.108453	20.11
18439	Brontothere indet.	Washakie	Wyoming	Uintan	41.438055	-108.268333	17.82
2023-TBR-08	*Lepisosteus*	Bridger	Wyoming	Bridgerian	41.21419	-109.66076	14.17 ±0.27
Gar Scale 1	*Lepisosteus*	Green River	Utah	Bridgerian	39.99842	-110.34760	15.41
2021-TBR-01	*Palaeosyops* sp.	Bridger	Wyoming	Bridgerian	41.094444	-110.182500	16.07 ±0.09
2023-TWl-17	*Telmatherium validus*	Lower Washakie	Wyoming	Bridgerian	41.10550	-108.14300	17.32 ±0.51
2023-TWl-22	*Telmatherium validus*	Lower Washakie	Wyoming	Bridgerian	41.10652	-108.14050	18.58 ±0.46
2023-TWl-23	*Telmatherium validus*	Lower Washakie	Wyoming	Bridgerian	41.09661	-108.15221	17.16 ±1.33

Table 3: Raw data received from the geochemistry lab at Utah State's Logan campus.

| Sample ID	$\Delta^{13}C$ VPDB	$\Delta^{18}O$ VPDB	$\Delta^{18}O$ SMOW
12762	-7.16	-13.59	16.90
18436	-7.46	-12.67	17.85
11023	-9.25	-12.23	18.30
11023r	-9.08	-11.40	19.15
11031	-8.61	-8.73	21.91
11032	-8.14	-10.02	20.58
11299	-7.60	-9.88	20.72
11299r	-7.98	-10.05	20.55
12335r	-9.01	-9.20	21.42
12335 (No Acid)	-9.56	-9.95	20.66
12349	-8.52	-9.87	20.73
12349 (No Acid)	-8.29	-9.10	21.52
13975	-8.37	-10.48	20.11
18439	-5.42	-12.70	17.82
18439b (No Acid)	-9.07	-9.93	20.68
2023-Tbr-08	-7.04	-16.51	13.89
2023-Tbr-08	-6.76	-15.97	14.44
Gar Scale 1	-6.76	-15.03	15.41
2021 TBR-01	-8.79	-14.49	15.97
2021 TBR-01b (No Acid)	-7.59	-14.30	16.16
2023-TWI-17	-5.77	-12.69	17.83
2023-TWI-17 (No Acid)	-6.13	-13.68	16.81
2023-TWI-22	-6.35	-12.19	18.35
2023-TWI-22	-6.58	-11.26	19.30
2023-TWI-22	-6.54	-12.48	18.04
2023-TWI-22 (No Acid)	-4.69	-11.93	18.61
2023-TWI-23	-7.28	-12.25	18.28
2023-TWI-23	-7.13	-11.89	18.65
2023-TWI-23 (No Acid)	-5.67	-14.88	15.57
2023-TWI-23 (No Acid)	-5.97	-14.34	16.12
+/-	0.11 (0.20)	0.15 (0.21)	
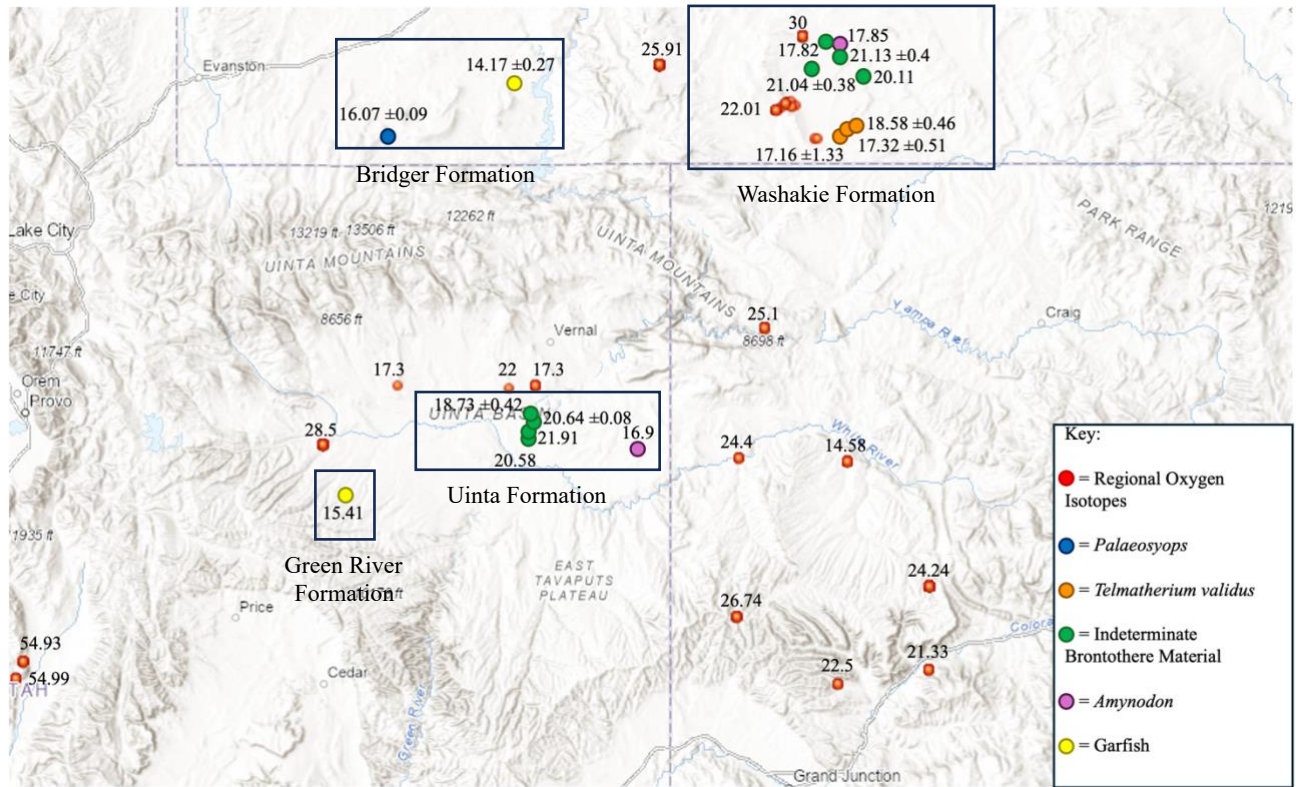
Figure 8: Map of the Uinta Mountains with sites indicating locations where specimens were discovered. Studied formations are labelled and identified. Regional carbonate isotopes from the PATCH Lab (2024) are shown for comparison with fossil values.
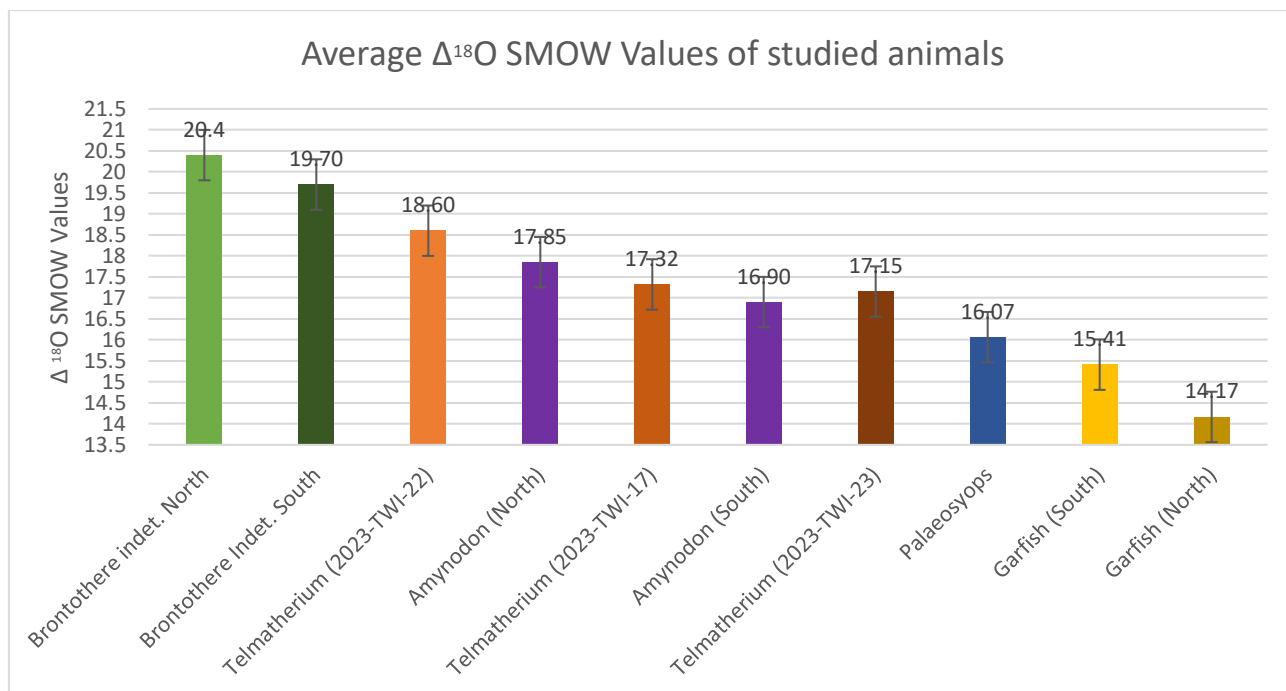
Figure 9: Average Δ^{18}O isotope values from Table 3. The *Amynodon*, garfish, and indeterminate brontothere, samples were split based on geographic range, which provides us with different values for both northern and southern specimens. The *Telmatherium* specimens were split based on the averages of individual specimens as they had the most values of the described genera. This way each *Telmatherium* specimen can be individually compared to other animals.

My results show little difference in specimens that were treated with acetic acid, with no disparity that could impact my conclusions (Figure 10). Specimens 18439 (indeterminate brontothere) and 2023-TWI-23 (*Telmatherium*) showed the greatest difference between treatment and no treatment. This could be the result of dust sneaking into the untreated samples, but nothing that would suggest extreme contamination. Due to how similar their treated values are to those of the other specimens, the treated value should be taken as more reliable.
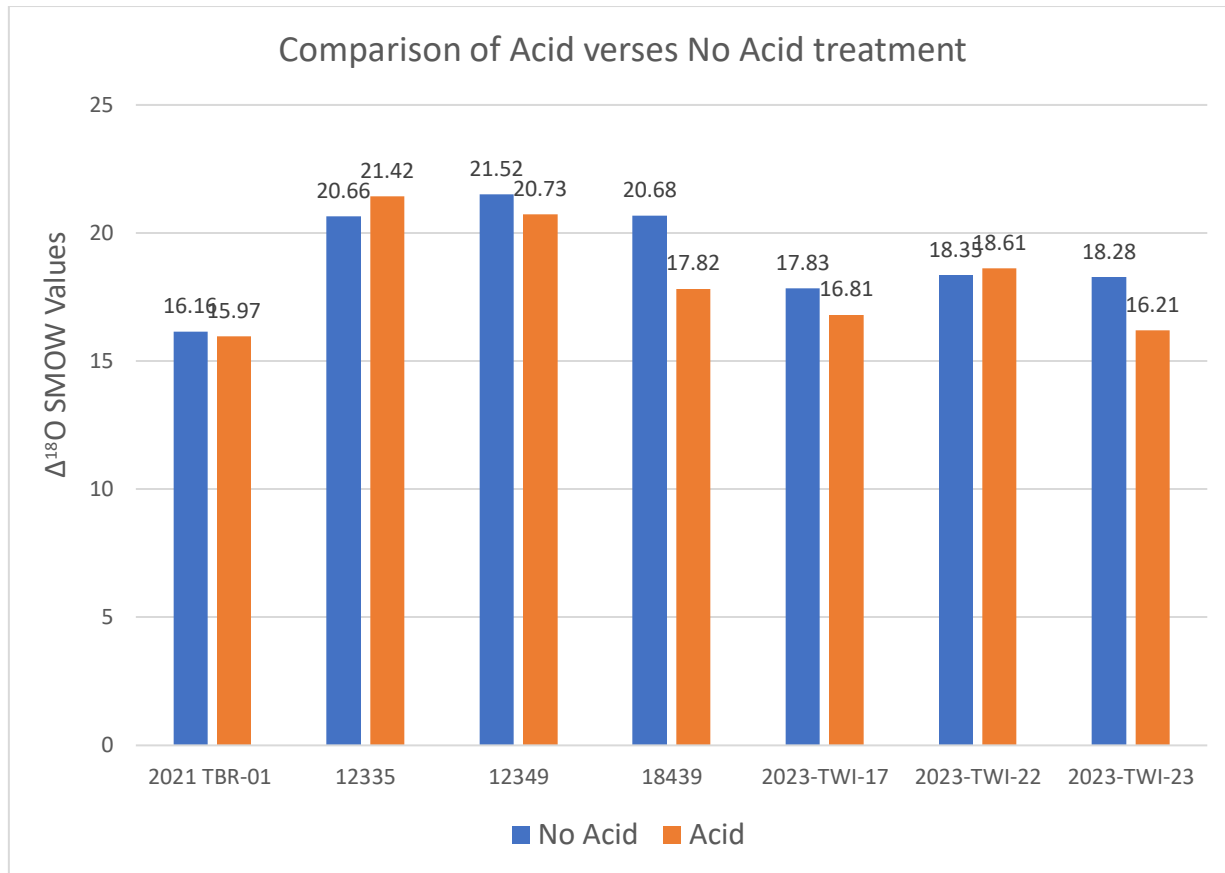
Figure 10: Comparisons between specimens that were both left alone and underwent acid treatment, showing little effect of calcite contamination except for 18439 and 2023-TWl-23.

Taking the average of the acid treated specimens, the Uintan brontothere material had an isotopic average value of 20.94, while the Washakie and Bridger brontotheres had an average value of 18.41‰ SMOW. This results in a difference of 2.53‰ SMOW. The gar scale values, 13.89-14.44‰ SMOW in the north and 15.41‰ SMOW in the south, present a difference of 1. Taking the lowest northern value and the highest southern value, the difference between them is 6.32‰ SMOW, while the highest northern value and the lowest southern value have a difference of 1.16. (show latitude difference)

The statistical test results showed a greater amount of variance in the *Telmatherium* specimens despite each being so close to one another (Table 4). Geographically there seems to be

little variance between the brontotheres on either side of the Uintas (Table 5) although variance is

dependent on sample size.

Table 4: Statistical table comparing the variance between analyzed species. The high variance for the indeterminate brontotheres is expected as they may represent a variety of different genera. *Telmatherium* has a noticeably high variance despite the specimens being in close proximity to one another in the Washakie Formation (Figure 5).

Species:	Brontothere indet.	*Telmatherium*
	18.3	17.83
	19.15	16.81
	21.91	18.35
	20.58	19.3
	20.72	18.04
	20.55	18.61
	21.42	18.28
	20.66	18.65
	20.73	15.57
	21.52	16.12
	20.11	
	17.82	
Variance:	**1.456190972**	**1.297604**

Table 5: Statistical table comparing the geographical differences between brontothere specimens. In total there appears to be little statistical variance between either side of the Uintas.

Species:	Northern Brontotheres	Southern Brontotheres
	21.42	18.3
	20.66	19.15
	20.73	21.91
	21.52	20.58
	20.11	20.72
	17.82	20.55
	15.97	
	16.16	
	17.83	
	16.81	
	18.35	
	19.3	
	18.04	
	18.61	
	18.28	
	18.65	
	15.57	
	16.12	
T-Test North-South **P ≥ 0.05**	**0.023**	

Chapter V: Discussion

5.1 Brontothere Water Dependency

My results show a consistent range in oxygen isotope values among my brontotheres that, when compared to previous research into oxygen isotopes of Eocene perissodactyls, are lower than those of the brontothere *Megacerops* (Figure 11). Compared to other perissodactyls from the Late Eocene White River Formation, *Megacerops*, referred by the junior synonym *Brontops* in this research, had a mean ^{18}O value of 23.0 ± 1.0% (Zanazzi and Kohn, 2008). This gives it the lowest

values for ^{18}O when compared to contemporary perissodactyls such as the early horse *Mesohippus* (24.2 ± 1.6%) and the rhinoceroses *Subhyracodon* (25.0 ± 1.3%) and *Trigonias* (26.9 ± 2.0%) (Figure 11). It has been interpreted therefore that *Megacerops* was more water dependent than other White River perissodactyls (Zanazzi and Kohn, 2008). However, *Megacerops'* comparatively low carbon-13 (^{13}C) isotope values suggests that it inhabited dense forests rather than open country. As a result, the increased humidity in these habitats, which decreases ^{18}O in leaf water, may also play a role in the lower ^{18}O values seen in their dentition (Zanazzi and Kohn, 2008).

The values in this report are strikingly lower for the Washakie, Bridger, and Uinta brontotheres than those of the White River's *Megacerops*. This could suggest that none of my brontotheres were more water dependent than the other. All, however, were more water dependent than *Megacerops* (Figure 11). The greater water dependency seen in Middle Eocene brontotheres compared to later species could be further explained by the habitat they lived in. Based on the paleoenvironmental interpretations of the Washakie, Bridger, and Uinta Formations, the lower isotope values seen in *Palaeosyops* align with the Bridger's interpretation of a humid forested habitat (Murphey et al. 2017). Given what we already know about the impact humidity can have on isotope values in later species, it is not unreasonable to suggest that a combination of water dependency and increased humidity resulted in low ^{18}O values in *Palaeosyops'* dentition. Likewise, the higher values in *Telmatherium* and other brontotheres from both the Washakie and Uinta Formations correlate well with the interpretations of comparatively drier habitats (Murphey et al. 2017; Tomiya et al. 2021). The fact that the values from southern Uinta Formation are closer to the northern Washakie despite being a more arid environment is intriguing and could suggest

that water dependency in brontotheres was high regardless of habitat. This distinction warrants

further exploration into the similarities of habitat between the two formations.
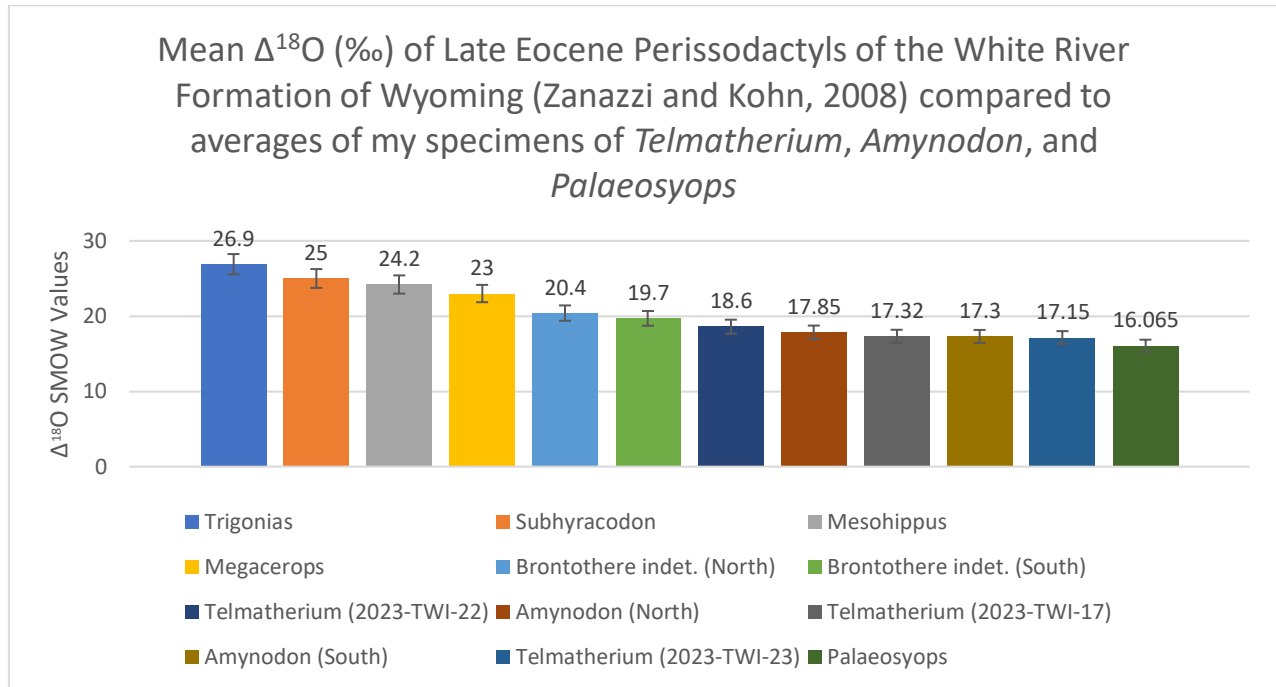

Figure 11: Mean $\Delta^{18}O$ values of perissodactyls from the Late Eocene of the White River Formation (Zanazzi and Kohn, 2008) compared with my specimens. *Megacerops* has the lowest value of the White River perissodactyls but is higher than my brontothere specimens. As with Figure 8, the indeterminate brontotheres, *Amynodon*, and garfish specimens are split by geography, while *Telmatherium* is split by specimen. This was done to prevent the *Telmatherium* data looking like a single extended bar on the graph.

5.2 Uinta Topography and Ecology During the Middle Eocene

In comparing the calculated averages and differences for both the southern and northern

brontothere specimens (20.94 and 18.41‰ SMOW respectively; difference of 2.53‰ SMOW)

with those of the southern and northern gar scales (15.41 and 13.89-14.44‰ SMOW respectively;

difference of about 1), the ratio values are lower on the northern face of the mountains (Figure 10;

Figure 11). This indicates the possibility that a rain shadow effect occurred in the Uintas during

the middle Eocene, with the northern side of the mountains receiving less precipitation than the

southern side. For comparison, the oxygen isotope difference between the ice-capped Alps meteoric water sources at 4,000 meters and the southern coast of Italy near the ocean at 2,000 meters is about 6‰ SMOW, and the difference between the lower Apennine Mountains and the Mediterranean coast is between 3 to 4‰ SMOW (Giustini et al. 2016). The Uintas therefore may have been topographically closer to the Apennines during the Eocene than the current height of the Italian Alps. The modern Apennines themselves reach an elevation of 9,500 feet, while the Alps reach 15,500 feet. This is further supported by the geographic trend seen where the closer specimens are to the mountain range, the greater the difference between the north and south, representing source waters depleted in ^{18}O on the northern side of the mountain range (Figure 12). The geography of the Uintas and the Apennines differs in that the Apennines reside along the Italian peninsula while the Uintas are from continental North America. The presence of ancient lakes during the Eocene however provides sources of moisture that make them comparable for this study (Murphy et al. 2017).

The elevation of the Apennines also causes a rain shadow effect to take place. As a result, the western side of the mountains receives higher precipitation levels, ranging between 1,700 and 2,000 mm, than the eastern side, whose precipitation ranges between 700 and 900 mm (Allocca, Manna, and De Vita, 2013). The habitats on either side differ accordingly. To the north and west, forests made up of deciduous oak and chestnut trees predominate. The climate in these parts of the range is temperate oceanic in the uppermost elevations (Blasi et al. 2014). The central and southern Apennines meanwhile support forests of beech and elm trees as well as some natural grassland (Blasi et al. 2014). Floral patterns in the central Apennines also display similarities with Alpine "dry valleys" (Cancellieri et al. 2017). This has been attributed to the Apennine rain

shadow effect. A rain shadow is therefore likely to have existed during the Eocene in the Uinta

Mountains.
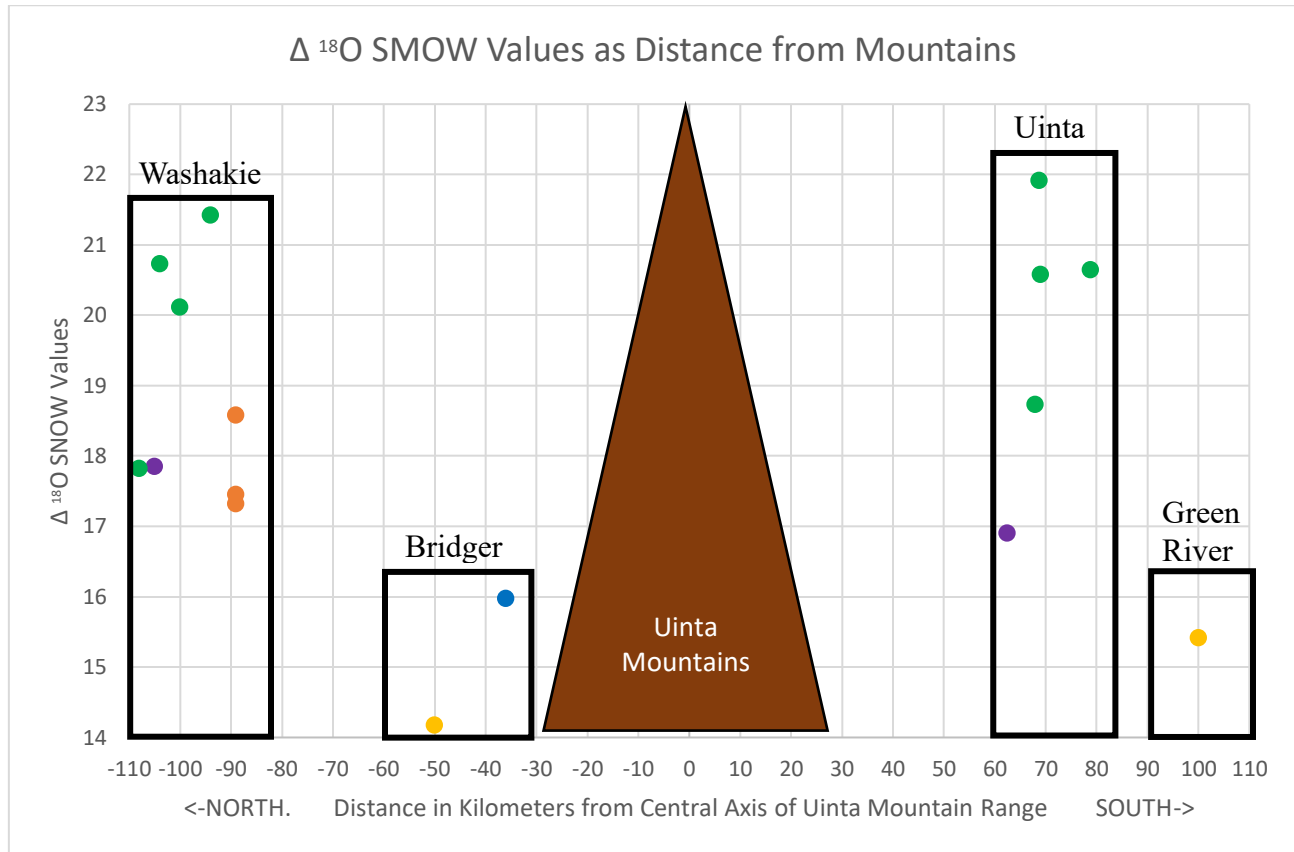
Figure 12: Comparison between studied formations and the brontothere and Amynodon values found at each. The Bridger's low values could be attributed to its proximity near the mountains. The color code goes as follows: Green = Indeterminate Brontothere, Orange = *Telmatherium*, Blue = *Palaeosyops*, Purple = *Amynodon*, and Yellow = Garfish.

Climatically however, neither side of the Apennine Mountains differs enough for their

habitats to be complete opposites of one another. Oaks and birches for example are also present in

the southern and central regions, and a temperate oceanic climate can be found in parts of the

southern and central regions (Blasi et al, 2014). This contrasts with rain shadows that result in

significantly different environments on either side. The Atacama Desert in northern Chile for

example resides west of the Andes Mountains and is the driest nonpolar desert in the world (Bull et al. 2018). Directly east of the Atacama are the Bolivian Yungas, a region of tropical montane forests (Gerold et al. 2008). The two habitats are diametric opposites when compared to those seen in the Apennines. The modern Uintas maintain a rain shadow with a 1.32 ‰ SMOW difference in oxygen isotopes in their surface water (Cite here). The low difference in this case makes direct comparisons between the modern Uintas and the Apennines difficult.

Like the Apennines, the Green River, Washakie, and Bridger Formations have roughly similar habitat interpretations that do not significantly deviate from one another, despite the rain shadow present. This adds support to a modestly high elevation of the Uintas during the middle Eocene that produced a mild rain shadow. Additional information on the types of plants that inhabited either side of the Uintas would help narrow down specific differences between botanical communities and paleoenvironments.

As mentioned previously, the Uinta Formation's unique savanna habitat appears to be the result of a general shift in climate and not due to the uplift of the Uinta Mountains for the time being. That is not to suggest that uplift did not contribute to this trend. Mountain building events during the Eocene, particularly in the Rocky Mountains, coincide with the slow decrease in temperatures during the middle Eocene (Townsend, 2004). Whether the Uinta Formation's savanna habitat is the result of this uplift will depend on further research into the evolution of the Uinta Mountains throughout the Eocene and beyond.

It should be noted that, based on my limited sample size, there appears to be a significant range of elevations that the Uinta Mountains could have been reached during the Eocene. The biggest difference that could be calculated, taking the lowest northern value (15.57 ‰ SMOW) and the highest southern value (21.91 ‰ SMOW), is 6.32 ‰ SMOW. This is significant as it

would indicate that the mountains could have reached Italian Alps elevations. This would suggest a very dramatic rain shadow being present. In the opposite extreme, the lowest southern value (20.58 ‰ SMOW) and the highest northern value (21.42 ‰ SMOW) produces a difference of 1.16 ‰ SMOW. This would suggest a low mountain range with little if any rain shadow. Consequently, there is a great uncertainty to the exact elevation of the Uintas during the Middle Eocene. While my T-test results using the brontothere isotopes supports the interpretation of a milder rain shadow given the low statistical variance between either side of the Uintas, the limited sample size remains a caveat. A much denser sample size would be required to best understand this geographic difference, which is impractical currently with the limited availability of fossils to study in museum collections.

5.3 Brontothere and *Amynodon* Biogeography and Paleoecology

5.3.1 Brontotheres

    Palaeosyops has the lowest isotope values of all my brontothere specimens (15.97-16.16 ‰ SMOW) and is the closest specimen to the mountain's axis (Figure 5; Figure 8; Figure 12). Compared to the other brontothere specimens, *Palaeosyops'* values are also the closest to the Bridger *Lepisosteus* specimen, which could indicate that *Palaeosyops* was possibly semi-aquatic. Alternatively, its preservation in a more upland area, where drinking water would have been more depleted in ^{18}O, may explain these low values. A modern example of this can be seen in Iberian Ibex that inhabit the Pyrenees Mountains in Spain. The closer they are to the mountains, the lower their oxygen isotope values become (Knockaert et al. 2018). This could also explain its rarity within basin centers in the Uinta and Washakie Formations, making it more localized to the

Bridger Formation closer to the mountains. This could suggest *Palaeosyops* preferred upland environments compared to its relatives.

Telmatherium meanwhile has much higher oxygen isotope values than *Palaeosyops*, which suggest it was a more terrestrial brontothere. Its preservation in the basins of the Washakie Formation (Figure 8), further away from the mountains, also suggests a preference for lowland habitats. Among the indeterminate brontothere specimens of my study, their values are either similar or much higher than in *Telmatherium*, indicating that they too may have been more terrestrial than *Palaeosyops*. Their presence in basins away from the mountains also suggests that, like *Telmatherium*, these brontotheres preferred lowland habitats (Figure 8). Further observation shows that neither these indeterminate animals nor *Telmatherium* intermingled in the same vicinity. This could suggest more specific habitat or dietary preferences that caused these animals to avoid living in large mixed species herds. Such possibilities warrant further investigation and study. For now, based on this geographic data, it can be argued that competition between different brontotheres was mitigated by habitat partitioning, enabling the diversity of genera we see in the fossil record.

5.3.2 Amynodon

The two *Amynodon* specimens for my study come from the Washakie and Uinta Formations, each on either side of the Uintas, but show little difference in isotope values (Table 2; Figure 9; Figure 12). When compared to most of my brontothere specimens, their values are lower, and in fact are closer numerically with the garfish values (Table 2). The most comparable brontothere to my *Amynodon* values is *Palaeosyops*. If *Palaeosyops'* lower values suggest a

semiaquatic lifestyle, then semiaquatic habits may have been exhibited in *Amynodon* as well. This is an interesting finding when compared to other research into amynodont biology. Although amynodontids are colloquially referred to as "swamp rhinos," suggesting the entire family was semi-aquatic, a previous study argued that only certain genera, such as the Late Eocene-Early Oligocene genus *Metamynodon*, were adapted for an amphibious lifestyle (Wall and Heinbaugh, 1999). This is based on physical adaptations in *Metamynodon* that closely resemble those in the extant Hippopotamus such as nostrils positioned high on the skull, a reduced lacrimal bone, and reduced neural spines (Wall and Heinbaugh, 1999). The result was two tribes of derived amynodonts: the semi-aquatic metamynodontines, and more terrestrial cadurcodontines (Wall and Heinbaugh, 1999; Averianov et al, 2017). *Amyndon*, a more basal member, was concluded to not have the characteristics necessary to support a semi aquatic lifestyle and was instead argued to have been a cursorial or subcursorial mammal (Wall and Heinbaugh, 1999).

However, the study also suggested that *Metamynodon* represents an extreme stage in amynodontid evolution towards being semi-aquatic (Wall and Heinbaugh, 1999). Combined with isotope values more comparable to *Palaeosyops* and ancient garfish than terrestrial brontotheres, *Amynodon* may have exhibited semi-aquatic tendencies even if it was not as specialized as *Metamynodon*. Further research into *Amynodon* and other members of the family is required to better understand these results and determine if other amynodonts not part of metamynodontini displayed semi-aquatic habits as well.

5.4 Interpretations of Brontothere Sociability

Although bonebeds made up of multiple brontothere individuals are known in the United States (Santos, 2018), none of my specimens were found in bonebeds or other mass death assemblage that would provide support for herding behavior based on the abundance of individuals in one small area. There is at least one documented bonebed of middle Eocene brontotheres from the Washakie Formation, made up of more than twenty partial skeletons belonging to *Mesatirhinus* (Turnbull and Martill, 1988). The individuals in the assemblage have been differentiated based on sex and age, with multiple males and females of various ages from juveniles to old adults. It has been suggested that the bonebed represents a herd or members of a larger herd of *Mesatirhinus* that were killed in a single event, possibly while crossing a flooded river. Mass death assemblages like this are rare among Eocene mammals in general and is especially rare among brontotheres as a group (Turnbull and Martill, 1988).

As seen in Caribou, similar oxygen isotope values among individuals suggest that they were part of the same herd and drank from the same water sources (Britton et al. 2009). Research into herding of possible early domestic sheep in a Neolithic site in Turkey showed statistical variance that can be compared to my brontothere data (Henton, 2011). The variance value in the sheep set was 0.45, which is lower than the variance values for either *Telmatherium* (1.30) and the indeterminate brontotheres (1.46). The statistical variance seen in the indeterminate specimens is unsurprising as their variation in oxygen isotope values is high, and suggestive of different genera among them. The *Telmatherium* variance value however is especially interesting as all three specimens were found close to each other in the Washakie Formation yet show greater variation in statistical variance and oxygen isotope values than expected. This appears to suggest that these individuals were not members of the same herd if compared to the Turkish sheep data (Henton,

2011). It's important to note however that this comparison is imperfect as the sheep herds may have been managed by Neolithic humans, and were not a completely natural occurrence (Henton, 2011).

Conclusions about the sociability in my brontothere specimens could be variable, as modern mammals today do not strictly choose between massive herds or solitary existences. Gaur, a type of Asian wild cattle, for example can range in group size from solitary individuals to herds of to 42 animals (Ramesh et al. 2012). Year-round, Gaur typically form groups of up to 10 individuals, but larger herds seem to form during the wet season due to increased food availability. During the dry season, it has been observed that a small contingent of adult bulls form bachelor herds while just under half of all bulls live solitary lived (Ramesh et al. 2012). Group sizes of the contemporary Asian Elephant meanwhile range from solitary animals to 22 individuals. Like the Gaur, most groups are made up between one and 10 individuals, although no seasonal variation among herds has been identified (Ramesh et al. 2012).

With relation to my data and specimens, the oxygen isotope variance provides evidence that the studied brontotheres may not represent members of the same group while not necessarily representing entirely solitary animals (Table 4). Although they are all relatively close numerically, the values deviate significantly when compared at an individual level. These disparities indicate that they were not members of a single organized herd. This leaves room for a variety of interpretations of social structure, suggesting that brontotheres may have had a wide range of social groups like modern Gaur and Indian Elephants.

Chapter VI: Conclusion

My research into brontothere social behavior and paleoecology using oxygen isotopic analysis has painted an extraordinary picture of the Uinta Mountains during the middle Eocene. The Uinta Mountains were a relatively high range that supported a mild rain shadow. This rain shadow was not severe enough to cause vastly different habitats to appear on either side, allowing for a range of environments to support animals including brontotheres both in the northern and the southern sides. That is not to say that my results conclude a definitive elevation for the Uintas during that time, however. Given the range of potential estimations shown with my specimens, a much larger sample size is necessary to narrow down a more accurate elevation of the mountain range.

The brontotheres in this report show variety in habitat preference and potential lifestyles that indicate a level of niche partitioning between species. This is especially valuable in understanding their diversity in the Eocene and their abundance in the Uinta Mountains. Many other research paths open with this preliminary data. Whether other brontotheres preferred upland habitats like *Palaeosyops* or more lowland basins like *Telmatherium* requires a greater number of specimens, ideally from confirmed genera, as well as further analysis of their oxygen isotopes. Carbon isotope analysis of brontotheres could also provide insight into niche partitioning among different genera based on diet. Additional research into brontothere sociability would benefit greatly from the discovery of other bonebeds, but as with habitat partitioning, a greater number of specimens could be analyzed to gauge social groupings among different genera. Research could also extend into social migration, a behavior that has recently been researched in the teeth of other extinct mammals, such as deer, horses, and woolly mammoths (Pellegrini et al. 2008; Kowalik et

al. 2023). These animals have shown patterns in oxygen isotope values that suggest seasonal variance over the course of their lives, and when compared to regional isotope values, suggests some level of migration. Whether this can be seen in brontothere teeth will depend on future research of their teeth.

The addition of the *Amynodon* specimens also opens paths to further research about their own ecology and evolution. As a basal member of Amynodontidae, the lack of derived characteristics that would support a semiaquatic lifestyle in *Amynodon* is a factor that needs to be considered despite the isotopic evidence suggesting they spent some amount of time in water. Oxygen isotope data from more *Amynodon* enamel specimens could flesh out this proposed lifestyle, or present alternative explanations for the low oxygen isotope values. Additionally, oxygen isotope data from genera across Amynodontidae can provide insight into the evolution of semiaquatic lifestyles in the family leading to the more derived Metamynodontids.

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