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Paleobiological and paleoclimatological significance of stable isotope patterns across early Eocene Hyracotherium tooth rows

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Paleobiological and paleoclimatological significance of stable isotope patterns across early Eocene Hyracotherium tooth rows

Abstract
The main objective of this study was to determine the most reliable teeth in early Eocene Hyracotherium fossil tooth rows for paleoclimate reconstruction using delta18O values preserved in the tooth enamel. Specimens came from two localities within the Bighorn Basin of Wyoming, D-1204 and D-1583. ANOVA and T-test results generally indicate non-significant differences in mean and variance across tooth rows consisting of m/1, m/2, p/4, and m/3 adult teeth, suggesting any of these teeth may be used for paleoclimate reconstruction purposes as long as sample sizes are large. Additionally, two distinct isotopic patterns were observed across tooth rows, possibly representing late summer/early fall and spring birth seasons. This suggests that Hyracotherium may have given birth multiple times per year and/or could give birth during two different seasons. Such inferences about birth seasons, coupled with dietary delta 13C interpretations, also suggest alternating dry and wet seasons during the lifetime of these individuals.

Keywords
Paleoclimate Science, Paleoecology, Geochemistry, Geology
PALEOBIOLOGICAL AND PALEOClimatological significance
of stable isotope patterns across early eocene
Hyracotherium tooth rows

by

Abigail R. D’Ambrosia
B.A., Smith College, 2007

Thesis

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ABSTRACT

PALEOBIOLOGICAL AND PALEOCLIMATOLOGICAL SIGNIFICANCE
OF STABLE ISOTOPE PATTERNS ACROSS EARLY EOCENE
HYRACOTHERIUM TOOTH ROWS
by
Abigail R. D’Ambrosia
University of New Hampshire, September 2012

The main objective of this study was to determine the most reliable teeth in early Eocene Hyracotherium fossil tooth rows for paloclimate reconstruction using $\delta^{18}$O values preserved in the tooth enamel. Specimens came from two localities within the Bighorn Basin of Wyoming, D-1204 and D-1583. ANOVA and T-test results generally indicate non-significant differences in mean and variance across tooth rows consisting of m/1, m/2, p/4, and m/3 adult teeth, suggesting any of these teeth may be used for paloclimate reconstruction purposes as long as sample sizes are large. Additionally, two distinct isotopic patterns were observed across tooth rows, possibly representing late summer/early fall and spring birth seasons. This suggests that Hyracotherium may have given birth multiple times per year and/or could give birth during two different seasons. Such inferences about birth seasons, coupled with dietary $\delta^{13}$C interpretations, also suggest alternating dry and wet seasons during the lifetime of these individuals.
CHAPTER I

INTRODUCTION

For decades, stable isotopes found in vertebrate fossils have been used to interpret paleoenvironments and paleobiology of fossil organisms (Koch et al 1992, Bryant et al 1996a, 1996b, Fricke & O’Neil 1996, Balasse et al 2002, Balasse et al 2003, Fricke & Wing 2004, Secord et al 2008, 2010). For example, oxygen and carbon isotopes in fossil mammal teeth have been used to interpret paleotemperatures, paleohydrology, and paleoecology. However, these studies are often complicated by animal physiology. For instance, tooth formation timing and behaviors such as nursing can lead to inter-tooth variability in oxygen isotope ratios. Considering such variability, this study will determine which teeth in the jaw of the earliest equid, *Hyracotherium*, are most reliable for use in paleoclimate reconstruction of the early Eocene. *Hyracotherium* teeth will be the main focus of this study due to the abundance of their fossils found in early Paleogene stratigraphy, which encompasses evidence of some of the most extreme greenhouse gas caused climate change events in Earth’s history (Gingerich 2006).

Longinelli (1984) was one of the first to understand the relationship between oxygen-isotope ratios in the body water of mammals and the oxygen-isotopes in the water they ingested. He realized that oxygen-isotope fractionation between ingested water and body water were species-dependent, and also that the isotope ratios of body water vary linearly with the ratios of local meteoric water. He determined that these
ratios are also recorded in bone and proposed that past oxygen-isotope ratios of ancient meteoric waters could be recorded in fossils. Luz et al (1984) were able to corroborate Longinelli’s conclusions, but went further to formulate a more detailed model of oxygen-isotope fractionation between ancient meteoric water and mammal fossils—incorporating mammal water-consumption and respiratory habits.

Since the oxygen-isotope ratios of meteoric water are related to atmospheric temperatures (Dansgaard 1964, Rozanski et al 1993), many studies have attempted to reconstruct paleotemperatures using mammal fossils. One such study, by Fricke and Wing (2004), set out to determine mean annual temperatures (MAT) across North America in the early Eocene using mammal teeth. They combined a physiological model developed by Kohn (1996) with oxygen-isotope fractionation equations developed by Longinelli and Nuti (1973) to determine ancient atmospheric temperatures from the isotope values recorded in fossil mammal teeth. Fricke and Wing corroborated their isotope-estimated temperatures with independent temperature estimates from standard paleobotanical methods.

In addition to oxygen isotopes as paleotemperature proxies, carbon isotopes have also served as paleoenvironmental proxies, through tracking variations in the carbon cycle, as well as recorders of animal diet. Koch et al (1992) was the first to correlate marine records of early Paleogene (circa 56 mya) global warming events to terrestrial records through use of an oxygen- and carbon-isotope stratigraphy developed from fossil mammal teeth and carbonate soil nodules (see also Secord et al 2010, Abels et al 2012). Carbon isotope ratios in mammal teeth have also been used to determine past mammal diets, and thus, the local habitat structure such as forest canopy type (Secord et al 2008).
It is important to understand the basic biology of an organism that is being targeted for isotopic study. For example, different teeth within a mammal jaw develop at different times and rates (Hilison 1986, Bryant et al 1996a, 1996b, Hoppe et al 2004). As a result, various teeth within a single mammal jaw may also record different isotopic signals. Previous studies have sought to determine the most reliable mammal teeth for paleoclimate reconstruction (Bryant et al 1996a, 1996b, Fricke & O’Neil 1996). For instance, by looking at isotope variation across horse, bison, and sheep tooth rows, as well as within individual teeth, it was concluded that later forming teeth are usually best for paleoclimate reconstruction purposes (Bryant et al 1996a, 1996b, Fricke & O’Neil 1996, Balasse 2002). The later-forming premolars and molars are ideal as they form after the animal has weaned and moved onto an adult diet. Thus, the teeth record no isotopic contamination from already fractionated isotopes in mother’s milk. These late-forming teeth also exhibit the least variation in isotopic values when compared to other teeth in the same jaw (Bryant et al 1996a, 1996b, Fricke & O’Neil 1996).

Bryant et al (1996a) was the first to go a step further and use the intrajaw isotope patterns to determine past birth cycles in groups of fossilized individuals. Such interpretations were corroborated by Fricke and O’Neil (1996), who found similar patterns after performing intratooth analysis on a modern bison and sheep. Balasse et al (2002, 2003) also performed similar intratooth analyses in steers and sheep, again able to interpret past birth cycles.

This study applies similar analyses to mammal teeth found from the early Eocene, beginning at about 56 million years ago. This period in Earth’s history is characterized by large-scale atmospheric carbon dioxide injections (Cramer et al 200, Lourens et al
2005, Bowen et al 2006, Gingerich 2006, Zachos et al 2008, Stap et al 2009, 2010, Abels et al 2012), and thus, it is crucial to understand how atmospheric temperatures and biota of terrestrial environments were affected at that time. Despite the pertinence of determining which mammals and which teeth are the best for making reliable paleoclimatological interpretations, it has not yet been done for one of the most commonly appearing mammal fossils of this time in the early Eocene—Hyracotherium. For this reason, Hyracotherium teeth will be the focus of this study.

**Research Objectives**

Although the paleoecology and paleobiology of Hyracotherium is relatively well known, no systematic analysis of variation across tooth rows has yet been carried out. This is surprising, as Hyracotherium is one of the most common fossils found in some of the best-preserved and most continuous early Eocene terrestrial stratigraphic sections in the world. Thus, the goals of this study are as follows:

1. Perform oxygen and carbon isotopic analysis across Hyracotherium tooth rows from known species and well sampled fossil localities. This will help to understand species-specific isotopic patterns.

2. Determine if the mean isotopic value of teeth vary systematically across the tooth row and find out which teeth consistently exhibit the least amount of isotopic variation. The tooth positions that exhibit the least amount of variability are ideal for use in developing paleoclimate and paleotemperature records as they minimize variability associated with biological effects and thus isolate the climate signal.
3) Decipher any other potential isotopic patterns across tooth rows. Aside from temperature information, oxygen isotopes in teeth may offer insight into birth cycles. Carbon isotopes may also offer insight into an animal’s dietary behavior.
CHAPTER II

BACKGROUND

_Hyracotherium_

_Hyracotherium_ is an ideal fossil to carry out palaeoenvironmental and palaeoecological analysis of the early Eocene, as it is one of the most commonly appearing fossils in some of the best continental stratigraphic sections of its time. _Hyracotherium_ is one of the earliest horses, appearing abruptly in the fossil record across northern continents at the onset of the Eocene, about 55.8 million years ago (Gingerich 2006, Rose 2006, Wood 2009). It was first discovered in England in 1838, where Sir Richard Owen first named it. Thirty-eight years later in 1876, another paleontologist, without realizing, found fossils of the same organism and referred to them as _Eohippus_, or the “dawn horse.” Although the fossils of _Eohippus_ were much more abundant in North America, subsequent studies by later paleontologists confirmed that the two genera were the same, and the name _Hyracotherium_ prevailed (MacFadden 1992). _Hyracotherium_ is now considered to be one of the oldest and most primitive equids (i.e., horses; Rose 2006).

_Hyracotherium_ is part of a larger order of mammals known as perissodactyls, or “odd-toed” ungulates (including modern day horses, tapirs, and rhinoceros). Perissodactyls first appeared at the onset of the Eocene along with artiodactyls (even-toed ungulates), and primates (Gingerich 2006). The earliest perissodactyls were
characterized by their elongate snouts, distinctive molars, and specialized skeletons for running (Radinsky 1969, Rose 2006).

Perissodactyls include a major group of mammals known as Equoids, which are further divided into two clades: equids (i.e., horses), and the closely related palaeotheres (early equoids from Europe; figure 2.1). *Hyracotherium* is the first and oldest of the equids (Rose 2006). Characteristics that led paleontologists to assign *Hyracotherium* to Equidae include the derived condition of an optic foramen and foramen ovale (i.e., cranial openings for optic and mandibular nerves). These features are shared with modern horses (Rose 2006).

![Figure 2.1. Cladogram depicting relationship of equoids (palaeotheres + equids) to other perissodactyls. *Hyracotherium* is considered the earliest equid, and by some accounts, may be more closely related to palaeotheres (Froelich 2002, Rose 2006). Image modified from Rose 2006.](image)

Recent phylogenetic analyses have suggested that *Hyracotherium* may actually be more closely related to palaeotheres than to equids (Froelich 1999, 2002, Rose 2006). With this in mind, Froelich (2002) proposed six different names for species once
considered to be of the *Hyracotherium* genus: *Pliohippus, Eohippus, Protorohippus, Sifrhippus, Minihippus,* and *Arenahippus*. However, the anatomical differences are so small that even experts have trouble distinguishing the newly proposed genera. Nonetheless, it is for certain that these “new” genera are some of the earliest Equoids (Rose 2006).

Depending on the species, *Hyracotherium* body size has been estimated to range between 4 and 35 kilograms—the smallest being around the size of a house cat (Gingerich 1981, MacFadden 1987, Rose 2006). They had longer limbs relative to other mammal groups in the early Eocene (although shorter compared to modern day standards), and with four toes on the forefeet and three in the back (Rose 2006). Their teeth were low-crowned (brachydont dentition), and designed for compressive chewing, or “crushing” (figure 2.2; Rose 2006, MacFadden 1992). Such eating styles were ideal for a diet of fruits, seeds, and tender leaves (Rensberger et al 1984, Janis 1990, MacFadden 1992). These speculations on diet were confirmed by the discovery of a late Eocene equid, *Propalaeotherium*, which had preserved evidence of grape pits in its fossilized stomach (Koenigswald & Schaarschmidt 1983, Franzen 1985, MacFadden 1992). MacFadden (1992) went further to speculate that *Hyracotherium* may have fed on a greater variety of vegetation, such as herbaceous dicots, woody shrubs, specialized ferns, and early, less abrasive grasses. *Hyracotherium* has been compared to the yellow-backed duiker of western Africa for its dietary behavior and dental-wear characteristics (Solounias & Semprebon 2002, Wood 2009).
Figure 2.2. Example of a Hyracotherium lower right jaw fragment used in this study. From left to right is the third premolar, fourth premolar, first molar, second molar, and third molar. Note the low-crowned brachydont dentition.

Hyracotherium is thought to have been a sexually dimorphic genus, as one species has shown to exhibit significant bimodality in cranial size and canine robustness (Gingerich 1981). A large fossil assemblage suggesting a low male/female ratio (1:1.5-2) may even suggest they were gregarious. This idea coupled with likely sexual dimorphism may mean they were also polygynous, much like modern-day horses (Gingerich 1981, Wood 2009).

**Geological Setting & Background**

All Hyracotherium specimens used in this study come from two localities in the Bighorn Basin of Wyoming (D-1204 and D-1583) and were collected by the U.S. Geological Survey between the years of 1977-1979, and by the U.S.G.S.-Johns Hopkins University School of Medicine expeditions between 1980-Present (figure 2.3; Bown et al
Fossils were collected from lag accumulations on topographic flats, or at the bases of small hills and slopes. According to Bown et al (1994), care was normally taken to keep surficial fossil collection within tight stratigraphic bounds, in the interest of “stratigraphic conservation.” The specimens in this study were borrowed from the National Museum of Natural History in Washington D.C., where they have been housed since their collection. All specimens used in this study are from the lower jaw of *Hyracotherium* due to the greater height of these teeth compared to upper molars and premolars, which allows for the collection of more material for isotopic analysis (see chapter 3 for a detailed discussion of the sampling procedures).

The Bighorn Basin is a Laramide-style foreland basin located in northwest Wyoming. It is located about 60 miles to the west of Yellowstone, and bordered by the Bighorn Mountains to the east, Beartooth and Absorakas to the west, and Owl Creek range to the south. This area is an ideal location to study the early Paleogene time period, as it exposes some 4,500 meters of the world’s best-studied stratigraphically continuous Paleocene and Eocene continental sedimentary deposits (Gingerich 1983, Bown et al 1994, Gingerich 2001, Kraus 2001).
The specimens in this study specifically come from the early Eocene Willwood formation which reaches a thickness of up to 1,400 meters. The Willwood formation is an alluvial deposit composed mainly of channel sandstone bodies, mudstones, and
highly-oxidized brightly colored paleosols (oranges, reds, and purples; Clyde 2001, Gingerich 2001). Irregular-shaped carbonate nodules are often found dispersed throughout the paleosols, formed by precipitation of micrite in soil channels (Gingerich 2001, Kraus 2001). The paleosols in the Willwood Formation suggest a well-drained fluvial system with open and relatively dry floodplains, likely deposited when accumulation exceeded subsidence in the basin (Clyde 2001, Gingerich 2001).

The paleoclimate of the Bighorn Basin during the early Eocene is suggestive of a warm-temperate to subtropical paleoenvironment (Wing et al 2000). Combined information from oxygen isotopes of mammals and fish have been compared with paleobotanical analyses to interpret atmospheric temperatures of at least 26°C during the warmest phase of the early Eocene (Fricke & Wing 2004). In 2008, Secord et al used carbon isotope values found in mammal tooth enamel to interpret diet, and thus infer habitat structure. They confirmed that woodlands prevailed, but isotopic values further suggested an open-canopy forest environment.

Many fossils are found within the Willwood formation. Fossil assemblages are dominantly composed of vertebrate faunas such as turtles, crocodiles, and mammals (Gingerich 2001). These fossils are common in thick superpositional stratigraphic sequences that can be traced laterally for kilometers (figure 2.4). With so many fossils and vast amounts of sedimentary deposition, evolutionary trends of various faunas can be traced through time in great detail. Plant fossils are also common, including palms, monocots, dicots, and ferns (Harrington et al 2001, Wing et al 2005).
Specimens from the D-1204 locality, known as "Kraus Flats," were first discovered in 1976 between 438 and 444 meters above the base of the Willwood Formation (figure 2.3). They were found across three paleosols of intermediate maturity, specifically of paleosol stages between 3 and 3+ (Bown et al 1994). Maturities of paleosols range on a scale between 0 to 6, with the level of maturity depending on soil thickness and development. They are thought to be proportional to the relative lateral distance from current stream-channel deposits (Bown 1985, Bown & Kraus 1987, Kraus 1987, Bown & Kraus 1993, Bown et al 1994). This locality lies within the Fifteen-Mile Creek master section measured by Bown between 1981 and 1982.

Specimens from the D-1583 locality, or "Bownanza," were first discovered in 1984. This locality is about 551 meters above the base of the Willwood formation, and also considered to be at a paleosol stage of 3+ (figure 2.3). This was considered a "locally very productive" locality, and placed in line with Schankler's 1980 Antelope Creek – Elk Creek – Buffalo Basin section (Bown et al 1994).
Figure 2.4. Willwood Formation deposits located in the central part of the Bighorn Basin. Individual stratigraphic sections can span hundreds of meters. Bright reds and oranges represent highly-oxidized paleosols, while the lighter colors represent sandstone layers or immature paleosols.

Why Teeth?

Tooth enamel is composed of the mineral hydroxyapatite, or “bioapatite,” with the formula of \( \text{Ca}_3(\text{PO}_4, \text{CO}_3)\cdot\text{OH} \) (Balasse 2002, Balasse et al. 2002). Enamel bioapatite is a particularly reliable recorder of oxygen isotopes because it is less susceptible to diagenetic processes over time. The moment that bioapatite is deposited, it can no longer be modified by biological or physiological processes. The chemical composition and isotopic ratios present during formation are essentially “locked in” (Fricke 2007). This is true for materials such as tooth enamel, tusks, and some reptile and fish scales. Bone, on the other hand, can be remodeled over a lifetime, leaving isotopic ratios that more likely reflect the average conditions closer in time to the animal’s death (Luz et al. 1990, Kohn & Cerling 2002, Fricke 2007).
Compared to other common fossil materials such as bone, dentine, and tusks, the larger crystal size of enamel bioapatite is less vulnerable to diagenetic alteration due to a larger surface area and decreased porosity potential (Fricke 2007). Porosity potential is defined by the amount of organic collagen present, which is easily altered or removed after burial. With less porosity and less crystal surface area exposed, isotopic exchange with surrounding fluids or addition of secondary apatite or carbonate is less likely (Zazzo et al 2004, Fricke 2007). For instance, unaltered bone is composed of very small bioapatite crystals (on the order of tens of nanometers), along with ~35% total collagen. Dentine, the soft material found beneath hard enamel in teeth, is also composed of small bioapatite crystals, but with less collagen (around ~20%). Enamel is composed of the largest crystals (hundreds of nanometers in length), along with less than ~5% collagen. These differences in bioapatite-collagen composition greatly influence the porosity of the material, and thus the quality of preservation (Kohn & Cerling 2002, Fricke 2007).

Oxygen Isotopes as a Temperature Proxy

All chemical compounds with stable isotope compositions are characterized by individual stable isotope ratios (such as oxygen and carbon in the interest of this study). These varying ratios are the result of preferential fractionation of different masses of the same atom (Sharp 2007). For example, oxygen comes naturally in three different isotope forms: $^{16}\text{O}$ (the most common isotope), $^{17}\text{O}$ (the least common isotope), and $^{18}\text{O}$. Oxygen isotope ratios are usually reported using the $\delta$ ("delta") notation, representing the ratio between the “heavy” $^{18}\text{O}$ isotope and the “light” $^{16}\text{O}$ isotope. The $\delta^{18}\text{O}$ value is calculated with the following equation:
\[ \delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000, \text{ reported in parts per thousand (‰)} \]

Where \( \delta \) stands for the abundance of the heavy to the light isotope (Sharp 2007). In the case of oxygen, the “standard” is V-SMOW (the Vienna Standard Mean Ocean Water). Carbon-isotope ratios (\( \delta^{13}C \), comparing \( ^{13}C \) to \( ^{12}C \)) are calculated with the same formula, with the standard usually being V-PDB (Vienna Pee Dee Belemnite).

For this study, understanding the \( \delta^{18}O \) of terrestrial surface waters is key in order to interpret atmospheric paleotemperatures. In modern day, \( \delta^{18}O \) in surface waters varies from 0‰ to -30‰. Negative values can be the result of “rain out” effects of the heavier molecules, or the preferential incorporation of heavier molecules into condensate where they are removed from cooling air masses (figure 2.5a). For example, during times of increased global warmth, more evaporation would be expected to occur over the oceans, and thus more \( ^{18}O \) incorporated into molecules of water vapor in clouds. As the clouds travel across cooling latitudinal gradients or large landmasses, precipitation occurs and \( ^{18}O \) is preferentially removed from that air mass (figures 2.5b & 2.5c). Thus, the more \( ^{18}O \) that is rained out onto land causes an increase in \( \delta^{18}O \) values of terrestrial meteoric waters. The less precipitation of \( ^{18}O \) out of an air mass might imply cooler atmospheric temperatures (Dansgaard 1993, Rozanski 1993).

Eventually, these cooling air masses precipitate out over landscapes into streams, rivers, ponds, lakes, etc. However, it is local hydrologic processes and environments that will contribute to the final isotopic signal (Fricke 2007). For example, humid areas may have water bodies with isotopic values that are representative of the original precipitated isotopic ratio, whereas dry areas are susceptible to additional evaporation and preferential
removal of the lighter isotopes. It is also important to take into account the influx or passing of waters from other areas (Sharp & Cerling 1998).

It is these surface waters that are likely ingested by local organisms and control the $\delta^{18}O$ values of their body water. Oxygen-isotope ratios found in vertebrate bioapatite are primarily determined by ingested water and atmospheric oxygen, which then contribute to the animal’s blood and metabolic water (Kohn 1996, Kohn & Cerling 2002, Frick 2007). However, since atmospheric oxygen has remained relatively constant over time at ~23%, it likely does not influence isotope ratio fluctuations in vertebrate teeth (Kohn 1996, Fricke 2007). Consequently, $\delta^{18}O$ fluctuations are most likely controlled through fractionations that occur during the formation of body water from ingested water, and by body temperature (which controls the fractionation between body water and apatite; Bryant & Froelich 1995). Where body temperature is known and constant, both of the above-mentioned fractionation factors can be considered together to estimate local meteoric $\delta^{18}O$ through physical models that account for the fluxes of oxygen into and out of the body and fractionations associated with each process (figure 2.6; Bryant & Froelich 1995, Kohn 1996).
Figure 2.5. Schematic diagrams showing how oxygen isotope ratios of air masses and land masses change with elevation and latitude (from Fricke 2007): a) Lighter isotopes are preferentially evaporated from the ocean and incorporated into travelling air masses. Thus, the air masses over the ocean have a more negative $\delta^{18}O$ value than the ocean. b) Heavier isotopes are preferentially precipitated out of progressively cooling and condensing air masses as they travel across higher latitudes and elevations. Their precipitation should have a higher $\delta^{18}O$ value than their associated air mass for this reason but the air masses will become progressively more negative. c) The relationship between latitude and precipitating $\delta^{18}O$ values. As latitudes increase, less $^{18}O$ is available to be removed from cooling air masses in the form of precipitation (Rozanski et al 1993). Figures from Fricke 2007.

In summary, the $\delta^{18}O$ of body water tracks the $\delta^{18}O$ of ingested local meteoric water, which is ultimately influenced by local temperatures and precipitation (Longinelli 1984, Balasse et al 2002, Fricke 2007). Higher values of $\delta^{18}O$ in enamel are generally observed in association with higher temperature climates, and lower values of $\delta^{18}O$ are observed with cooler temperatures (Bryant et al 1996a).
Assuming a mammal is drinking local meteoric water, $\delta^{18}O$ values from water will be incorporated into teeth as they grow. Consequently, the $\delta^{18}O$ values from mammal tooth enamel can be substituted into a physiological model to determine the $\delta^{18}O$ of meteoric water that has not been measured directly. These $\delta^{18}O$ values of water can be combined into a fractionation equation with the $\delta^{18}O$ values of something that precipitates according to temperature dependent equilibrium with water (i.e., enamel scales from a fish), finally determining the water temperature, $T$ (assumed to reflect atmospheric temperatures). Figure from Fricke 2007.

Kohn et al (1998) performed oxygen isotope analyses on the teeth of modern herbivores in Kenya, with a focus on seasonality and its use for assessing paleoclimates. They determined that seasonality, not developmental physiology, was indeed the likely explanation for variations in isotopes across teeth. For instance, gazelles, dik-diks, and zebras of east Africa exhibited $\delta^{18}O$ values within individual teeth (i.e., teeth were large enough for serial sampling across the growth axis) that could be explained by seasonal shifts between high $\delta^{18}O$ meteoric water values of the dry season and low $\delta^{18}O$ values of the wet season.

*Hyracotherium* likely acquired a significant amount of its body water through its diet, which likely consisted of leaves and other vegetation in open-canopy forests. Such vegetation is quite susceptible to evaporative enrichment, especially during warm and
arid conditions (Levin et al 2006, Secord et al 2012). Thus, *Hyracotherium*’s body water could have been particularly sensitive to dry conditions, and such environmental changes could be translated into tooth enamel isotope values.

Lastly, Sharp & Cerling (1998) investigated whether the turnover rate of $\delta^{18}$O in mammal body water could be so slow as to buffer $\delta^{18}$O ultimately recorded in the tooth enamel. They were able to determine that, for modern equids, the turnover rate is rapid enough to record monthly scale changes. They went further to suggest that the turnover rate could also be somewhat body size dependent. As a final point, they cautioned against using the teeth of mammals that were drinking out of buffered water sources (i.e., ponds, lakes, and large rivers), as this could also buffer the isotopic ratios.

**Tooth Development**

Teeth mineralize beginning from the crown to the base within many herbivorous mammals, meaning the oldest portion of the tooth is at the crown and the youngest at the base (figure 2.7). The enamel and dentine form at a common junction at the crown of the tooth, and grow away from each other towards the base of the tooth through time (enamel growing outwards; Hillson 1986, Kohn & Cerling 2002). Because teeth grow in this manner, the growth axis may actually reflect seasonal changes in $\delta^{18}$O values, as well as dietary changes in $\delta^{13}$C values over time. In essence, the continuous formation of enamel creates a time series of stable isotope ratios associated with the life history of the animal (Sharp & Cerling 1998, Kohn & Cerling 2002, Fricke 2007).
Figure 2.7. Simplified diagram showing the process of teeth mineralizing from top to bottom (youngest enamel is always at the base of tooth, whereas oldest is towards crown). Enamel grows out and away from the dentine. Ultimately, the growth axis represents a time series of stable isotope ratios. Figure from Fricke 2007.

Understanding the order and timing of tooth eruption in modern and fossil equids is crucial as it may help to sort out seasonal isotopic patterns across tooth rows. In modern horses, the first molar (m/1) erupts at about 7-12 months, the second molar (m/2) at 16-24 months, the second and third premolars (p/2 and p/3, respectively) at about 2.5-3.5 years, and finally the fourth premolar and third molar (p/4 and m/3) at 3 to 5 years (see figure 2.8; Bryant et al 1996a & 1996b). However, mineralization of the tooth enamel may occur over a year prior to eruption, which increases the likelihood of earlier developing teeth, such as m/1, mineralizing in vitro with the mother’s body water or under the influence of nursing (Bryant et al 1996, Fricke et al 1996). Both cases pose the risk that the mineralizing and erupting tooth enamel reflect already fractionated isotopes of the mother’s body water. This would lead to higher isotope values than those of the locally ingested meteoric water due to metabolic processes (Fricke et al 1996).

Furthermore, despite the longevity of mineralization and eruption of teeth in modern

1 A lower case “m” or “p” followed by a slash mark and a number represents a tooth from the animal’s lower jaw. Uppercase letters followed directly by a number (and sometimes a slash mark) indicate teeth from the upper jaw.
horses, Hillson (1986) estimated that for smaller animals the entire process could take only weeks to months.

**Figure 2.8.** Timing of enamel mineralization and tooth eruption within the same jaw of a modern horse or zebra. Note that mineralization was suspected to begin several months prior to eruption. Figure modified from Bryant et al (1996a).

While the above-mentioned eruption-timing and pre-weaning mineralization effects remain true, Hoppe et al (2004) investigated precise timing and spatial patterns of enamel mineralization using radiographic and optical analyses of juvenile and adult domestic horse teeth. They found that the timing of enamel mineralization takes much longer than previously thought. Specifically, enamel mineralization was found to continue well after tooth eruption, contrary to previous beliefs (Bryant et al 1996a, 1996b). Total enamel mineralization times ranged from about 1.5 to 2.8 years depending on the tooth. The m/1 mineralizes in about 22-23 months, the m/2 in about 30 months, the p/2 in ~18 months (the shortest mineralization time of all the premolars and molars), the p/3 similar to the m/1 at about 22-23 months, and finally the p/4 and m/3 mineralizing at about 32 and 34 months, respectively (figure 2.9; Hoppe et al 2004).
Hoppe et al (2004) was also able to confirm the two stages of enamel mineralization: “stage 1,” matrix production, and “stage 2,” enamel maturation (Hillson 1986, Kohn & Cerling 2002, Balasse 2002, Hoppe et al 2004), when a majority of the mineralization actually occurred (Hoppe et al 2004). Hillson (1986) estimated that the amount of organic matrix incorporated into the first phase of mineralization was around 30%, and was progressively replaced with dense and compact enamel over time. In her study of *Bos Taurus* (a steer), Balasse (2002) found that the early developing enamel was composed of about 80-90% organic matter, and reduced to only 10-20% in the “stage 2” mature enamel.

![Figure 2.9](image-url)  
**Figure 2.9.** More recently proposed timing of tooth eruption (grey dashed lines) and enamel mineralization (solid black lines) in modern horses, as determined through radiographic and optical analyses in Hoppe et al (2004). Note how mineralization often continues past tooth eruption, especially within the molars. Slightly modified from Hoppe et al (2004).
CHAPTER III

METHODOLOGY

Sample Preparation

Prior to the removal of enamel for isotopic analysis, the length and width of every tooth crown was measured using Fowler-Sylvac Ultra-Call Mark III digital calipers. All results were reported to the hundredths of the millimeter. This was done in the case that inferences of body size were needed. Mean tooth area for a given taxon can be used to estimate body size through established taxon-specific body size–tooth size regressions (like those of Legendre 1989; also see Morgan et al 1995, Clyde and Gingerich 1998).

Next, teeth were inspected for signs of alteration. Teeth that were extremely altered were automatically excluded from sampling. A tooth was considered to have minor alteration issues if portions of the enamel showed discoloration, often as a lighter grey-blue or white-tan spotting (figure 3.2). These teeth were still sampled, but excluded from statistical analysis and interpretations. Notes were always kept on the condition of these samples prior to isotopic analyses. Teeth that were very worn down, where enamel seemed unusually thin, or where there was uncertainty in the assigned tooth position, were also always noted. Such features could potentially distort the average isotopic signal across the tooth, and were therefore excluded from statistical analysis and interpretations.
Tooth enamel was removed using a Foredom k.2230 Flex Shaft rotary drill with diamond tip burrs. To obtain mean values of $\delta^{18}O$, enamel from the molars was removed in sections along the growth axis. Between 3 and 4 milligrams of enamel powder collected from drilling were pre-treated with NaOCl for 24 hours and rinsed 5 times with deionized water in order to remove any organic matter. The samples were spun dry in a RevSpin centrifuge for 15 to 20 seconds between each rinse. Next, the enamel powders were treated with 1M buffered acetic acid (with pH ~4.5) for 24 hours and rinsed 5 times to remove any diagenetic carbonates (following methods of Koch et al 1997). The samples were then dried in a 60°C oven for several hours.

**Laboratory Analysis**

Most of the D-1204 locality samples were analyzed at the University of Wyoming Stable Isotope Facility (excluding samples AD009B, AD013B, AD013C, AD021B, AD022A, and AD022B). About 1.5 milligrams of the enamel powders were weighed out
and then analyzed using a Thermo Finnigan Delta\textsuperscript{plus} XP continuous-flow isotope-ratio mass spectrometer with attached GasBench autosampler. All remaining samples were analyzed at the University of Arizona Environmental Isotope Laboratory using a Finnigan MAT 252 gas-source isotope ratio mass spectrometer with attached Kiel III automatic sample preparation device. The powdered samples were reacted with dehydrated phosphoric acid at 70\degree C. The final isotope ratio measurement was calibrated through repeated measurements of the NBS-18 and NBS-19 standards. The 1-sigma precision for $\delta^{18}$O measurements is $\pm 0.1\%_o$, and $\pm 0.08\%_o$ for $\delta^{13}$C.

All measurements from both labs were reported in per mil notation with respect to the V-PDB standard for carbonates. $\delta^{18}$O results were converted to V-SMOW using the following equation (Sharp 2007): $\delta^{18}$O\textsubscript{SMOW} = 1.03091 ($\delta^{18}$O\textsubscript{PDB}) + 30.91.

**Statistical Analyses**

Statistical analyses were performed through the JMP 9.0 software program. For each specimen locality, tooth isotope values were organized into groups by their associated tooth position within the jaw. The statistical analyses chosen for these data were based on the idea that the most reliable teeth for paleoclimate reconstruction should exhibit similar mean values to each other and the least amount of isotopic variation (see chapter 1).

Because isotopic variation across tooth position groups is the main focus of this study, "analysis of variance," or ANOVA, testing was the most appropriate statistical method. ANOVA consists of an F-test, which compares the variance of different distributions, whereas a T-test individually compares the means of different groups to see
if they are equal. The Student’s T comparison t-test is able to perform several pairwise
group analyses at once. All tests within this study were performed with a 95%
confidence level (α = 0.05).

Alternative tests for unequal variance were also always performed: the O’Brien,
Brown-Forsythe, Levene, and Bartlett tests. If one of these tests finds significant
inequality in group variances, an alternative ANOVA test statistic, known as Welch’s
test, is necessary. Welch’s test is more valid under unequal variance circumstances, and
is based on the usual F test. However, the main difference is that the group means are
weighted by the reciprocal of the group variances (JMP 9.0, 2010).

Statistically, the general null hypothesis for all tests is that all tooth positions
would yield non-significantly different isotopic values (that is, all mean values and
variance would be the same). On the other hand, the alternative hypothesis is that at least
one tooth position group would yield significantly different results from the others.
Details of results from all tests performed are available in appendices B, C, and D.

Finally, in order to draw any reasonable conclusions from the D-1204 or D-1583
data analyses, it is important to first consider the amount and quality of the data. For
instance, the D-1204 dataset is relatively small so more data may be needed to confirm
observed patterns in that sample set. On the other hand, the D-1583 data set has a
reasonably good sample size. However, the conclusions drawn from the p/3 teeth of D-
1583 are based on data from only three unquestionable specimens and thus must be
considered preliminary.
CHAPTER IV

RESULTS

D-1204 Locality Results

$\delta^{18}$O Analyses

For the D-1204 locality, an apparent pattern is observed with m/1 generally exhibiting lower $\delta^{18}$O values than the m/2s (figure 4.1). The m/1s have a mean value of 21.28% with a standard deviation of 0.95, while m/2s have a mean value of 22.15% with a standard deviation of 1.26. The m/3s, when not considering samples noted to be questionable due to signs of alteration, exhibit the lowest and least variable $\delta^{18}$O values (mean of 18.77% and a standard deviation of 0.24). It is important to note that an insufficient number of premolars were analyzed to draw any reasonable conclusions.

A one-way analysis of $\delta^{18}$O values versus tooth position was run with a Student’s T comparison test ($\alpha = 0.05$). The m/3 teeth yielded statistically different isotopic mean values compared to all of the other teeth (p-values were all less than 0.05, see appendix A for more details). The p/4 teeth were also shown to be significantly different than m/1s (p-value = 0.0108) although only one p/4 was included in this sample set.

The Levene test for unequal variances was also performed and was found to be significant (Prob > F = 0.0427, i.e., the probability that the null hypothesis is true). In response, the Welch’s test was performed and also found significance in variance (Prob >
Figure 4.1. Oxygen-isotope results from the D-1204 locality, separated by tooth position, in order of formation (order of formation begins with the m/1 on the left side of the plot). An incomplete sequence (meaning an individual tooth was unable to be sampled from the associated tooth row) is represented by a dotted line. Note the small variance in m/3s when excluding the "questionable" samples from analysis. Also note the lack of premolars in this set of data.

δ13C Analyses

δ13C values for the samples from D-1204 exhibit a similar inter-tooth pattern to the δ18O values. For instance, the m/1s exhibit lower δ13C values compared to their associated m/2s (figure 4.2). The first molars have a mean value of -12.83‰ with a standard deviation of 0.37, whereas m/2s have a mean value of -11.75‰ with a standard deviation of 0.55. Again, not enough data was available to draw conclusions from the premolars, but m/3s do seem to be lower in value (at least compared to m/2s). However,
the data yield more variable results for the m/3s. The m/3s exhibited mean $\delta^{13}C$ values of -12.67\%o and a standard deviation of 1.42.

![Graph of $\delta^{13}C$ of Hyracotherium Tooth Rows from the D-1204 Locality](image)

**Figure 4.2.** Carbon-isotope results from the D-1204 locality, divided by tooth position, in order of formation. An incomplete sequence (meaning an individual tooth was unable to be sampled from the associated tooth row) is represented by a dotted line. Note the larger variance across m/3s in this data set. Again, premolar samples are lacking in this group of data.

An analysis of variance yielded no statistical difference across the tooth position groups, but a Levene Test for unequal variance did find statistical significance in variance in at least one of the groups (this type of test does not specify which group). However, a Welch's test, performed in response, did not find any statistical significance in variance (Appendix C). A Student’s T test comparing mean values showed that the only significant differences among the teeth were between m/1s and m/2s (p-value = 0.0237).
**D-1583 Locality Results**

**δ¹⁸O Analyses**

For the D-1583 locality, the overall data yield no striking differences in mean values, with a slightly, but statistically insignificant, higher variance for m/2s (figure 4.3). First molars yield a mean δ¹⁸O of 22.04‰ and a standard deviation of 1.16, p/4s yield a δ¹⁸O of 21.84‰ and a standard deviation of 1.63, and m/3s a mean of 22.34‰ and standard deviation of 1.63. The m/2s show a similar mean of 22.00‰, but a relatively higher standard deviation of 2.17. Finally, p/3s exhibit a much higher mean isotopic value of 24.40‰ (with a standard deviation of 1.63). However, this last result is questionable as it only comes from three samples.

**δ¹⁸O of Hyracotherium Tooth Rows from the D-1583 Locality**

*Figure 4.3.* Oxygen-isotope results from the D-1583 locality, grouped by tooth position, in order of formation. An incomplete sequence (meaning an individual tooth was unable to be sampled from the associated tooth row) is represented by a dotted line. Note the relatively similar variances and means across the teeth, except for the p/3 that has a significantly higher mean (but is represented by a sample of only 3 specimens).
A one-way analysis of the $\delta^{18}O$ values versus tooth position was run with a Student's T comparison test ($\alpha = 0.05$). As expected, the only teeth to show a significant difference from the others were the p/3s (all p-values were less than 0.05, see appendix B for more details). No other test for equal variances found significant results. Thus, all tooth position groups with n>3 show similar, non-significantly different, means and variances.

$\delta^{13}C$ Analyses

Complementary to the results from D-1204, the D-1583 $\delta^{13}C$ values exhibit a similar pattern to the $\delta^{18}O$ values across the same tooth rows (figure 4.4). Again, the m/2s exhibit the most variance (mean of -12.13‰, standard deviation of 1.13), and the p/3s show the highest mean values (mean of -11.54‰, and standard deviation of 1.20). All other teeth show similar isotopic patterns to each other. The m/1s have a mean value of -12.31‰ and standard deviation of 0.60, p/4s a mean of -12.11‰ and standard deviation of 0.88, and m/3s a mean of -12.32‰ and standard deviation of 0.51.

An analysis of variance of the $\delta^{13}C$ data yielded no statistical difference across the tooth position groups, but a Brown-Forsythe Test for unequal variance did find statistical significance in variance in at least one of the groups (this type of test does not specify which group). In response, a Welch's test was performed and found no significance in variance (see appendix c). A Student's T test comparing mean values suggested that there was no significant difference between values of any group.
Figure 4.4. Carbon-isotope results from the D-1583 locality, grouped by tooth position, in order of formation. An incomplete sequence (meaning an individual tooth was unable to be sampled from the associated tooth row) is represented by a dotted line. Notice that the spread of data under each tooth category is very similar to the oxygen-isotope results from the same locality.

Apparent Isotopic Patterns of D-1583 Data

Oxygen-isotope data from specimens of D-1583 seems to show two distinct isotopic patterns. Specifically, “pattern A,” where the m/1s exhibit higher $\delta^{18}O$ values than the m/2s, and “pattern B,” where the m/1s exhibit lower isotopic values than the m/2s. Differences were taken between these m/1 and m/2 isotope values across all jaws, and then analyzed for their distribution. Bimodality was found, supporting the existence of the two distinct patterns (see figure 4.5; statistical details can be found in Appendix E).

In pattern A, the remaining premolars and m/3 also exhibit higher isotopic values than the m/2s, resulting in a “concave up” look (figure 4.6). The m/1s obtain a mean value of
22.31\%o and standard deviation of 0.98, p/3s a mean value of 24.40\%o and standard deviation of 0.79, p/4s a mean of 22.41\%o and standard deviation of 1.55, and m/3s a mean of 22.40\%o and standard deviation of 1.61. The m/2s have a mean value of 20.95\%o, a standard deviation of 1.48, which is significantly different from the m/1s, p/3s, and p/4s (p-values of 0.0306, 0.0007, and 0.0358, respectively).

**Figure 4.5.** The existence of bimodality in the difference between m/1 and m/2 isotope values is indicative of two different isotopic patterns. The x-axis of this figure bins the spread of m/1-m/2 isotopic values, while the y-axis counts the frequency of these values. Two modes are found, one at -1.32\%o, and another at 2.01\%o.

Pattern B displays the opposite in oxygen-isotope behavior. In addition to the m/1s being lower in $\delta^{18}O$ values, the p/4s and m/3s were also lower (there were no p/3 samples for pattern B), resulting in a "concave down" look (figure 4.7). The m/1s had a mean value of 21.22\%o and standard deviation of 1.40, p/4s a mean value of 20.71\%o and standard deviation of 1.25, and m/3s a mean of 22.26\%o and standard deviation of 2.03.
The m/2s have a mean value of 24.36% and standard deviation of 1.49—significantly different from m/1s and p/4s (p-values of 0.0141 and 0.0062, respectively).

Figure 4.6. In pattern A, m/2s tend to have lower isotopic values than the rest of the teeth. Note the "concave up" pattern between the m/1s and later-forming teeth.

Figure 4.7. In pattern B, m/2s tend to have the highest isotopic values compared to the other teeth. Note the "concave down" shape between the m/1s and most later-forming teeth.
Interestingly, carbon-isotope values seem to follow similar trends for each pattern with m/1s having higher $\delta^{13}$C values compared to m/2s in pattern A, and m/1s having lower $\delta^{13}$C values compared to m/2s in pattern B (figures 4.8 and 4.9). This observation is further confirmed by comparing the $\delta^{18}$O values with the $\delta^{13}$C values (figure 4.10). Pattern A yields an r-squared correlation of 0.4877 (ANOVA F-value < 0.0001). Pattern B yields an R-squared correlation of 0.4177 (ANOVA F-value < 0.0001). Detailed results of the statistical analyses can be found in Appendices C and F.

**Figure 4.8.** In almost all cases, the teeth and tooth rows that were assigned to pattern A by oxygen-isotope patterns also follow a similar pattern with $\delta^{13}$C values. Note the distinct drop in isotope values between m/1s and m/2s. The remaining teeth show slightly higher values than the m/2s, lending to a slight concave-up pattern.
Figure 4.9. For the most part, the teeth and tooth rows that were assigned to pattern B by oxygen-isotope patterns also follow a similar pattern with $\delta^{13}C$ values. Note the increase in isotope values from m/1s to m/2s. The remaining teeth have slightly lower values than the m/2s (although more data would be ideal to make such a determination with better confidence), lending to a concave-down pattern.

Figure 4.10. A significant correlation is found when plotting the $\delta^{18}O$ values against the $\delta^{13}C$ values. Pattern A is indicated by the red circles, while pattern B is indicated by the blue triangles. The regression line for pattern A is also in red ($\delta^{13}C = -20.3361 + 0.3719 \times \delta^{18}O, r^2 = 0.4877$), while the regression line for pattern B is in blue ($\delta^{13}C = -18.5934 + 0.2846 \times \delta^{18}O, r^2 = 0.4176$).
Considering Altered and Questionable Teeth

Comparing isotopic values of altered teeth to isotopic values of pristine teeth is important for knowing how careful one must be in choosing pristine teeth for paleoclimatic studies. Complete data analysis results are available in Appendix D. A list of the altered and questionable samples can be found in Appendix A.

For D-1204, the mean $\delta^{18}O$ value of the dataset excluding altered and questionable samples ("pristine" samples) was 21.55%, with a standard deviation of 1.92. The dataset composed only of slightly altered and questionable samples had a mean of 19.83%, and a standard deviation of 2.83. The pristine $\delta^{13}C$ data yielded a mean of -12.40%, with a standard deviation of 0.89, while the $\delta^{13}C$ data composed of the altered and questionable samples had a mean of -12.78%, and a standard deviation of 0.54. No statistical tests found and significance in variance or means across this dataset (figure 4.11a; see Appendix D for details).

For D-1583, the mean $\delta^{18}O$ value of the pristine dataset was 22.20%, with a standard deviation of 1.70. The data composed of the altered and questionable samples had a mean of 22.44%, and a standard deviation of 1.58. The pristine $\delta^{13}C$ data yielded a mean of -12.17%, with a standard deviation of 0.85, while the $\delta^{13}C$ data composed of the altered and questionable samples had a mean of -12.30%, and a standard deviation of 0.83. Similar to D-1204, there was no significant difference found among the group means or variance (figure 4.11b; see appendix D for details).
Figure 4.11. Comparison of mean $\delta^{18}$O and $\delta^{13}$C values for each location (plotted within two standard deviations). Figure A compares data for the D-1204 locality, while figure B compares data from the D-1583 locality. Blue lines, noted as "pristine," do not include the altered and questionable samples. Red lines, labeled as "slightly altered," include only the slightly altered and questionable samples. There was no significance found between the slightly altered vs. pristine datasets for either locality, note the overlap in both figures. This suggests that slight alteration does not affect overall results and interpretations.

Ultimately, there were no major differences found between the datasets that excluded altered and questionable samples and the datasets that included such samples. This implies that specimens with slight visual alteration can be included in paleoclimatic studies given that they do not seem to significantly affect the results. Given the relatively small size of the D-1204 and D-1583 datasets, interpretations in this study do not include such altered and questionable samples as a precaution, however the results do not differ when data from these slightly altered samples are included (Appendix D). Also, it is important to note that strongly altered specimens were not sampled at all in this study and should always be avoided given the likely effects of diagenesis.
CHAPTER V

DISCUSSION

Tooth Enamel for Paleoclimate Reconstruction

One of the main objectives of this study is to determine which teeth in a *Hyracotherium* tooth row exhibit the least amount of isotopic variation, and thus will act as a consistently reliable proxy for the δ\(^{18}\)O of ingested surface waters and the δ\(^{13}\)C of the diet. When collecting specimens in the field, it is common to find individual teeth, rather than in association with a jaw. Given this, the results from the entire D-1583 dataset are probably the most relevant for interpretations, as it would be impossible to know which inter-tooth isotopic pattern (A or B) a single tooth belongs to when found in the field. Additionally, the D-1583 dataset is better sampled compared to D-1204, and the D-1204 results do not contradict the D-1583 results in any significant way. Results of the D-1583 dataset show no teeth, aside from p/3s (which may not be a reliable sample due to their small sample size), are significantly different from each other in terms of variance. Just as important and somewhat unexpectedly, none of teeth vary systematically from one another in terms of their mean values. Such results suggest that m/1s, m/2s, p/4s, m/3s, and possibly p/3s of *Hyracotherium* found in the field may all work as reliable proxies for δ\(^{18}\)O\textsubscript{ingested water} and δ\(^{13}\)C\textsubscript{diet}.

The δ\(^{18}\)O values from the early Eocene equids of this study exhibit slightly higher variance than δ\(^{18}\)O values found in Miocene horse jaws of the Bryant et al (1996a) study.
However, the greatest variance occurred in m/1s for Bryant et al (1996a), whereas the greatest variance from this study was seen in m/2s. The high absolute amount of variability observed in the carbon and oxygen isotope results for equids in general, however, makes it important to sample as many teeth as possible through the target stratigraphic section when carrying out such studies. This should not prove difficult, as *Hyracotherium* specimens are relatively common in the field.

![Figure 5.1](image)

**Figure 5.1.** A) Slightly modified from Bryant et al (1996a), this figure compares the range of oxygen isotope variations between Miocene horses from two separate localities (Burge quarry fossils are dated at ~12 Ma, Thomson Quarry fossils are dated at ~17 Ma). In general, it was found that m/1s exhibited the greatest amount of variation, while the later-forming teeth exhibited the least amount of variation. Note the difference in mean values across teeth. B) Isotopic variations from teeth measured in this study are highest among m/2s in the larger D-1583 dataset, although means and variance are not statistically significant across any of the tooth positions. Thus, any of these teeth would be equally valuable for paleoclimate use.
Life History

Reproductive Cycles

Bryant et al (1996a, 1996b), when conducting isotopic studies on the tooth rows of more recent extinct and extant equids, realized that the isotopic patterns seen across teeth in jaws represented birth seasons and seasonal cyclicities. For instance, high values in the first-forming m/1s followed by lower values in the m/2s within the same jaw meant that the animal was likely born in the spring, with the m/1 forming during warmer temperatures of spring through late summer, followed by the m/2 beginning formation between cooling temperatures of later summer to fall. The opposite pattern would be seen had the animal been born in the fall (figure 5.3).

Like the Bryant et al (1996a, 1996b) studies, many other studies have used the relationship between seasonal δ¹⁸O values of meteoric water or precipitation and variations in δ¹⁸O of tooth enamel to determine birth seasonality in fossil organisms. Birth seasons of fossil sheep from Kasteelberg, South Africa were determined from intratooth oxygen isotope analysis ("intratooth" meaning serial sampling across the growth axis of an individual tooth—a process that requires more sample material than a single *Hyracotherium* tooth can provide; Balasse et al 2003). The intratooth isotopic patterns exhibited evidence of two birth seasons for the sheep, one in the autumn and another in the spring. In modern Kasteelberg, autumn is the optimal time of year for feeding and lambing due to prospering shrubs from the autumn rains. The spring is a less favorable season for new births, but still plausible as it is also the time of year for shrub shoot growth and the completion of the local grass growth cycle. Both of these items are a dietary preference for modern sheep. Many other isotope studies have also suggested
multiple birth seasons for fossil organisms such as gazelles from Israel between 53 and 70 ka (Hallin et al 2012), and equids from the Siwaliks of Pakistan between 6.3 and 10 Ma (Nelson 2005).

Within this study there seems to be two distinct birth cycles, observed as pattern A and pattern B, showing up in both the D-1204 and D-1583 samples. To determine the precise birth seasons, both patterns were plotted along a seasonal isotope curve representing a likely seasonal range in $\delta^{18}O$ values (figure 5.2). This range in values was determined by isotopic intratooth sampling of Coryphodon tusks from a similar stratigraphic interval in the Bighorn Basin (isotopic data from Fricke et al 1998). Coryphodon tusks were ideal in this scenario as serial sampling could be performed along the entire growth axis of the tusk, capturing a full range of isotopic values throughout many seasons of the animal’s life.

Based on an isotopic curve representing a seasonal amplitude of 3.1%, the mean values for the Hyracotherium teeth in this study suggest the following birth seasons: Pattern A suggests a late summer/early fall birth, with both m/1s and m/3s being higher in $\delta^{18}O$ values than the m/2s (figure 5.2a). The slightly opposite isotopic scenario is found in pattern B, suggesting a spring birth season (figure 5.2b). The occurrence of multiple birth seasons may even explain the relatively high isotopic variance found in the teeth of this study (see figure 5.1 in the previous section). Evidence of multiple birth seasons suggests two possibilities for the reproductive behavior of Hyracotherium: 1) Small body size is conducive to multiple births per year, and/or 2) births could occur during one season or the other.
Figure 5.2. Seasonal isotope fluctuations in δ¹⁸Osub, enamel values of Coryphodon tooth enamel specimens from the same stratigraphic interval as the D-1583 Hyracotherium specimens in this study (gray curved line). The seasonal range in isotopic values as collected from the Coryphodon teeth was ~3.1‰. A) By plotting the Hyracotherium mean isotope values for each tooth position, pattern A suggests the formation of the m/1, and thus the birth of the associated animals, to be during the late summer to early fall. Completion of tooth formation occurred in ~1 year. B) The pattern B birth season is suggested to be during the spring months. Completion of tooth formation occurred in little over one year. The red dash line and arrow for the m/2 tooth position is indicating that the δ¹⁸O values were too high to fit on the curve. This may be due to the smaller sample size of the pattern B dataset.

Many studies in the past have shown a relationship between small body size and fecundity (that is, female reproductive success; MacFadden 1992). This reproductive success was seen in the form of greater numbers of litters per female, along with a greater number of littermates. Thus, fecundity factors for fossil equids would include body size and developmental timing, both interrelated. MacFadden further suggested that if
reproduction was not synchronized into breeding peaks, it was likely that the organism was able to produce more than one litter per year. *Hyracotherium* was proposed as a prime example due to its small body size.

It should also be stressed that examples of multiple birth seasons are common in modern faunas. For example, Penzhorn (1985) observed the reproductive performance of the Cape Mountain Zebra (*Equus zebra zebra*) over a period of 30 years. Out of 306 total observed births, 213 occurred in the summer, while 93 occurred in the winter. Similar behavior has been observed in Burchell's Zebra (*Equus burchelli antiquorum*), with a majority of the conceptions and births occurring in the summer (Smuts 1976). In these examples, the summer season also happens to be the wet season, when green vegetation is more readily available, having a profound effect on breeding activity (Smuts 1976, Penzhorn 1985).

**Body Size and Developmental Timing**

Hillson (1986) suggested that smaller animals develop their teeth faster than larger animals, perhaps in less than one year. Therefore, it is reasonable to imagine that *Hyracotherium*’s adult teeth were mineralized and erupted within the first year to year-and-a-half of age, as suggested by the tooth position timing on the *Coryphodon* seasonal isotope curves discussed in the previous section (see figure 5.2). Such timing is far less than that observed for modern horses at ~4 years (Bryant et al 1996a, 1996b, Hoppe et al 2004b).

Using established taxon-specific tooth size – body size regressions (Legendre 1986, MacFadden 1986), the average size of *Hyracotherium* first molars in this study was
calculated to represent a body size range between 7.46 and 23.10 kg (see Appendix G for further details and equations). More importantly, when body weight and tooth formation timing of various modern mammals are plotted together, a significant correlation is found (figure 5.3; $R^2 = 0.5825$, ANOVA F-test <0.0024). Using the regression equation suggested from this correlation, a *Hyracotherium* ranging in size between 7.46 and 23.10 kg is estimated to complete tooth formation within 1.24 to 1.95 years. This estimate further supports the 1-1.5 year tooth formation timing as suggested by the *Coryphodon* seasonal isotope curves.

**Figure 5.3.** This figure describes a range of modern mammalian body weights (converted to Log$_{10}$) and the associated ages at which final tooth eruption occurs. Note that as mammals become larger, tooth formation and eruption takes a longer time to complete. Using the regression equation developed from the modern mammal – body weight relationship, *Hyracotherium*’s estimated body weight predicts a 1.24 – 1.95 tooth formation time (as seen by red dot on plot).
General Interpretations for Carbon Isotope Patterns

When considering the carbon isotope patterns found across the *Hyracotherium* tooth rows in this study, interpretations of dietary behavior can be made, including interpretations about seasonal diet changes. Carbon isotope values found in herbivore tooth enamel should directly reflect the δ¹³C values found in the plants that are being consumed (Hoppe et al. 2004a, Fricke 2007). However, there is a natural offset between enamel isotopic values and diet isotopic values due to isotopic fractionations, leading to δ¹³C values in the enamel being significantly higher (Fricke 2007). This offset, or isotopic enrichment factor (ε*), was first reported to be about 14.1±0.5‰ based on a study of large-sized wild animals (figure 5.4; Ambrose & Norr 1993, Cerling & Harris 1999, Hoppe et al 2004a, Fricke 2007). However, Secord et al (2008) developed a similar equation based on smaller animals similar to those dwelling in the Bighorn Basin during the early Eocene. It was determined that for smaller, non-artiodactyls, ε*<sub>δ<sup>13</sup>C<sub>enamel-diet</sub></sub> equaled to ~13.1‰.

In this study, the D-1204 dataset yields a $\delta^{13}C_{\text{enamel}}$ range between -11.0 and -14.5‰, while the D-1583 dataset yields a $\delta^{13}C_{\text{enamel}}$ range between -10.0 and -14.5‰. When considering the enamel-diet offset, the carbon isotope values of both datasets fall within the same values as C$_3$ plants. Thus, these values suggest agreement with dietary behaviors of *Hyracotherium* as proposed by Rensberger et al (1984), Janis (1990), and MacFadden (1992), as well as $\delta^{13}C$ values of dispersed organic matter and fossil plants of the same time period and locality (Secord et al. 2008).

Another interesting observation from the carbon isotope data in this study is that the $\delta^{13}C$ patterns across tooth rows mimic the $\delta^{18}O$ patterns. For instance, when $\delta^{18}O$ is low, (i.e., cooler temps), $\delta^{13}C$ is also low. When $\delta^{18}O$ is high, (i.e., warmer temps), $\delta^{13}C$ is also high. A study conducted by Sharp and Cerling (1998) looked at various fossil horse specimens and also pointed out this striking coupled variation between $\delta^{18}O$ and

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*Figure 5.4.* Graph showing isotopic values in animal teeth compared to the isotopic values in the plants that those same animals were eating. Note the rough 14.1±0.5‰ offset (Kohn & Cerling 2002).
8\textsuperscript{13}C values within teeth. They determined that changes in the 8\textsuperscript{13}C of the fossil horse specimens were controlled by annual variations in the 8\textsuperscript{13}C of plants (with higher values associated with dryer conditions, as well as a diet that changed seasonally due to the availability of C\textsubscript{4} plants for consumption in the warmer summer months).

The data from this study suggest a similar explanation to the findings of Sharp and Cerling (1998). For instance, when 8\textsuperscript{18}O suggests cooler temperatures, 8\textsuperscript{13}C is lower, suggesting typical C\textsubscript{3} plants in Hyracotherium's diet. When 8\textsuperscript{18}O suggests warmer temperatures, 8\textsuperscript{13}C is higher, possibly suggesting C\textsubscript{4} plants that are growing in more arid conditions. As a reminder, high 8\textsuperscript{18}O values are also indicative of evaporative enrichment in leaf water that is ultimately ingested, further corroborating arid conditions indicated by 8\textsuperscript{13}C values (Levin et al 2006, Secord et al 2012). It is also possible that C\textsubscript{4} plants may have been introduced to the diet during dryer seasons. Although C\textsubscript{4} plants are not widely known in the early Eocene of the Bighorn Basin, plant fossils with living C\textsubscript{4} relatives are known from the Paleogene of this region (including cycads, certain aquatic lycopods, and certain pollens; Wing et al 1995, Wing & Harrington 2001, Secord et al 2008). However, this interpretation relies on further confirmation of the presence of C\textsubscript{4} plants.

In addition to general interpretations of seasonal 8\textsuperscript{13}C fluctuations of plants consumed by Hyracotherium, it may also be possible to interpret seasonal changes to the forest canopy, including potential fluctuations in precipitation patterns. Secord et al (2008) studied the 8\textsuperscript{13}C_{enamel} of several early Eocene forest-dwelling mammals of the Bighorn Basin and interpreted an open canopy forest for this area. They were further able to determine that these forests were densely vegetated and/or had high water
availability due to the $\delta^{13}C_{enamel}$ falling on the lower end of the range expected for open canopy forests. They pointed out that the natural variation in $\delta^{13}C$ of C$_3$ plants is due to environmental factors such as light, temperature, nutrients, and water availability. They noted how $\delta^{13}C$ in leaves decreased with increasing humidity or precipitation (Heaton 1999), and how $\delta^{13}C$ in leaves increases with increasing irradiance (Ehleringer et al 1986, Stewart et al 1995). Again, in this study, when $\delta^{18}O_{enamel}$ suggests cooler temperatures, $\delta^{13}C$ in the *Hyracotherium* teeth are also seen to be low. This decrease in $\delta^{13}C$ suggests a decrease in irradiance as well as an increase in humidity or precipitation. When $\delta^{18}O_{enamel}$ suggests warmer temperatures, $\delta^{13}C_{enamel}$ is higher. This increase in $\delta^{13}C$ suggests an increase in irradiance, along with a decrease in humidity or precipitation. It is possible that the *Hyracotherium* teeth are actually recording a “wet” season when the temperatures are cooler and $\delta^{13}C$ values are low. Conversely, the teeth may be recording a “dry” season when the temperatures are warm and $\delta^{13}C$ values are high.

High $\delta^{13}C$ values coupled with $\delta^{18}O$ values that represent warmer summer months are consistent with an increase in the $\delta^{13}C$ values of C$_3$ plants due to water stress in the summer or a possible increase in the consumption of C$_4$ plants. Interestingly, most of the specimens seem to be following isotopic pattern A, suggesting the warmer and/or dryer season for “foaling.” This is slightly different than for modern equids, including feral horses and zebras, which tend to give birth in the wet summer seasons (Smuts 1976, Penzhorn 1985) when $\delta^{18}O$ values are typically lower (Kohn et al 1998, Hoppe et al 2004a). The main reason why modern horses, zebras, and other larger mammals tend to foal during the wet season is due to the fact that they also breed during the same season a year earlier (gestating for ~1 year), likely triggered by new and lush growth for their diet
(Smuts 1976, Penzhorn 1985, Balasse et al 2003). If *Hyracotherium* was more likely to breed in the wet season (with low $\delta^{18}$O and $\delta^{13}$C values), it is possible that a shorter gestation period due to their small size would lead more of them to give birth in the following drier season with higher $\delta^{18}$O and $\delta^{13}$C values.
CHAPTER VI

CONCLUSIONS

Summary and Conclusions

The main objective of this study was to determine the most reliable teeth in a *Hyracotherium* tooth row for early Eocene paleoclimate reconstruction using oxygen isotopes. Teeth that showed the least amount of isotopic variance would be the most ideal candidates for such reconstruction purposes. Based on studies of late Eocene to Recent equids, variance was expected to be greatest across the earliest forming teeth (e.g. m/1) due to isotopic contamination from mother’s milk prior to weaning. Variance was expected to be smaller across adult teeth that formed later (e.g. m/3) when the animal was on a purely adult diet of vegetation and water reflecting local meteoric water δ¹⁸O values. These later-forming teeth generally take the longest to grow and should encapsulate a more seasonally-averaged “narrow” signal (Hillson 1986, Bryant et al 1996a, 1996b, Hoppe et al 2004b).

Results from this study of *Hyracotherium* suggest a much different pattern compared to these previous studies (Bryant et al 1996a, 1996b). All teeth across *Hyracotherium* tooth rows exhibit similar means and similar, but relatively high, variance in their δ¹⁸O enamel values (aside from p/3s which were very poorly sampled). These data suggest that several teeth of *Hyracotherium* are acceptable when sampling for paleoclimate reconstruction (at least those that were the focus of this study: m/1s, m/2s,
p/4s, m/3s, and possibly p/3s), so long as many teeth are sampled given the
generally high degree of variability for all of the teeth. In other words, for paleoclimatic
isotopic studies using *Hyracotherium* teeth, the tooth position does not seem to matter as
much as maximizing the total the number teeth analyzed.

Interestingly, two distinct oxygen isotope patterns were found across tooth rows
from both the D-1204 and D-1583 sampling localities. These are interpreted to represent
two distinct birth seasons for *Hyracotherium*—likely the late summer/early fall and the
spring months. It is unclear whether *Hyracotherium* was able to produce more than one
litter per year (which would be plausible due to its smaller body size), and/or if
*Hyracotherium* could give birth at any time in the year (MacFadden 1992). Today, many
small mammals are able to give birth multiple times per year, and some mammals are
able to give birth in any season of the year due to environmental factors such as reduced

Finally, $\delta^{13}$C analysis was also performed on the *Hyracotherium* teeth from this
study. Between both datasets, $\delta^{13}$C<sub>enamel</sub> ranged between -10.0 and -14.5‰. When
considering an enamel-diet offset of $\sim$13.1‰ (Secord et al 2008), carbon isotopic values
in tooth enamel clearly suggest that *Hyracotherium* consumed C<sub>3</sub> plants (which yield
$\delta^{13}$C values of $\sim$27+3‰; Hoppe et al 2004a). Furthermore, the range in values of $\delta^{13}$C
may be the result of environmental variables like humidity, which can cause $\delta^{13}$C of C<sub>3</sub>
plants to vary significantly (Secord et al 1008, Hallin et al 2012). For instance, $\delta^{13}$C
values of C<sub>3</sub> plants are higher during the hotter and dryer seasons due to decreased
isotopic discrimination during carbon uptake. Interpreting the $\delta^{13}$C in the context of the
$\delta^{18}$O results suggests the possibility of wet and dry seasons in the Bighorn basin. For
instance, a cool wet season is indicated by low $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, as low $\delta^{18}\text{O}$ suggests a cooler climate, and low $\delta^{13}\text{C}$ suggests increased humidity. The opposite values indicate a warm, dry season. Most birth cycle patterns in this study are suggestive of a warm and dry birth season, dissimilar to modern equids (Smuts 1976, Penzhorn 1985). This may be due to the fact that *Hyracotherium* bred in the wet season (similar to modern equids), and gave birth in the following wet season (as their small size and short lifespan likely mean they went through a short gestation period).

In conclusion, the most important result from this study is that m/1, m/2, p/4, and m/3 adult teeth from *Hyracotherium* tooth rows do not differ systematically in their carbon and oxygen isotopic values and thus should be equally reliable for palaeoenvironmental reconstruction. However, isotopic values are quite variable in an absolute sense so it is important to sample as many teeth as possible to reduce isotopic uncertainty. Additionally, inferences about reproductive behavior suggest that *Hyracotherium* was either able to give birth more than once per year and/or that it could give birth during two different seasons. Such interpretations about birth seasonality, coupled with inferences on changing $\delta^{13}\text{C}$ values, may also be useful in understanding more general palaeoclimatological patterns in the early Eocene of the Bighorn Basin, including palaeotemperature estimates, implications for reduced seasonality, and seasonal climate patterns.
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APPENDIX A

LIST OF SPECIMENS

Table 1: List of all specimens sampled. Altered and questionable specimens that were noted prior to sampling and excluded from analysis are labeled in bold.

<table>
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<td>C</td>
<td>-11.28</td>
<td>24.85</td>
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</tbody>
</table>

Excluded from analysis. Tooth very worn with thin enamel. Drilling powder peach in color.

Excluded from analysis. Many small areas of alteration. Attempted to drill through unaltered areas.

Excluded from analysis. Many small areas of alteration. Attempted to drill through unaltered areas.

Excluded from analysis. Definite surficial alteration.

Excluded from analysis. Drilling powder red in color.

Excluded from analysis. Enamel thin and worn. May have hit dentine while drilling.

Excluded from analysis. Enamel thin and slightly cracked. May have drilled dentine.
| D-1583 | 58A  | L m/3 | -12.23 | 21.81  |
| D-1583 | 58B  | L m/4 | -12.08 | 22.40  |
| D-1583 | 59A  | L p/4 | -11.40 | 22.81  |
| D-1583 | 59B  | L m/1 | -11.83 | 22.65  |
| D-1583 | 59C  | L m/2 | -12.06 | 21.12  |
| D-1583 | 60A  | R m/2 | -11.42 | 24.47  |
| D-1583 | 60B  | R m/3 | -12.60 | 22.33  |
| D-1583 | 61A  | R p/3 | -10.29 | 25.06  |
| D-1583 | 61B  | R p/4 | -10.86 | 24.24  |
| D-1583 | 61C  | R m/1 | -12.50 | 20.46  |
| D-1583 | 61D  | R m/2 | -13.62 | 19.16  |
| D-1583 | 61E  | R m/3 | -11.69 | 23.75  |
| D-1583 | 62A  | R p/4 | -11.78 | 20.62  |
| D-1583 | 62B  | R m/1 | -11.51 | 21.82  |

Excluded from analysis. Drilling powder yellow in color.

Excluded from analysis. Drilling powder yellow in color.

Excluded from analysis. Drilling powder slightly pink in color.

Excluded from analysis. Thin enamel, broke apart when drilling.
APPENDIX B

OXYGEN ISOTOPE STATISTICAL ANALYSES

Table 2. δ¹⁸O Statistical Analyses for ALL Locality Data Combined

Analysis of Variance

<table>
<thead>
<tr>
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<th>Prob &gt; F</th>
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Means for One way ANOVA

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<th>Stand. Dev.</th>
<th>Stand. Error</th>
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<tbody>
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Comparisons for Each Pair Using Student's T

<table>
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<tr>
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<th>Std. Err. Diff.</th>
<th>p-Value</th>
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<td>0.0326*</td>
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<td>m/3</td>
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<td>0.1614</td>
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Tests for Unequal Variance

| Level | Count | Stand. Dev. | |Mean| to Group| |Mean| to Group| |Median|
|-------|-------|-------------|----------------|-------|----------------|-------|
| m/1   | 22    | 1.1371      | 0.8957          | 0.8957 |
| m/2   | 19    | 1.8920      | 1.4763          | 1.4449 |
| p/3   | 5     | 2.0834      | 1.5679          | 1.6831 |
| p/4   | 14    | 1.9147      | 1.5395          | 1.5395 |
| m/3   | 10    | 2.1824      | 1.9333          | 1.9333 |

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<tr>
<th>Test</th>
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<td>Brown-Forsythe</td>
<td>2.5081</td>
<td>0.0504</td>
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Table 4. \( \delta^{18}O \) Statistical Analyses for D-1583

**Analysis of Variance**

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**Means for One-way ANOVA**

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<th>Stand. Error</th>
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**Comparisons for Each Pair Using Student's T**

<table>
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<th>Std. Err. Diff.</th>
<th>p-Value</th>
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**Tests for Unequal Variance**

| Level | Count | Stand. Dev. | Mean | Median | \( |Mean| to Group | \( |Mean| to Group |
|-------|-------|-------------|------|--------|--------|---------|---------|
| m/1   | 16    | 1.1566      | 0.9529| 0.9428 |
| m/2   | 13    | 2.1679      | 1.7123| 1.6657 |
| p/3   | 3     | 1.6294      | 1.2368| 1.1986 |
| p/4   | 12    | 1.6293      | 1.4180| 1.4180 |
| m/3   | 7     | 1.6349      | 1.2446| 1.2460 |

<table>
<thead>
<tr>
<th>Test</th>
<th>Ratio</th>
<th>Prob &gt; F</th>
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<td>Brown-Forsythe</td>
<td>1.0767</td>
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<td>Levene</td>
<td>1.4302</td>
<td>0.2391</td>
</tr>
<tr>
<td>Bartlett</td>
<td>1.2090</td>
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69
Table 5. $\delta^{18}O$ Statistical Analyses for D-1583, pattern A

*Analysis of Variance*

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<th>Prob &gt; F</th>
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</thead>
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*Means for One-way ANOVA*

<table>
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<th>Stand. Error</th>
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<td>m/3</td>
<td>4</td>
<td>22.4028</td>
<td>1.6052</td>
<td>0.6834</td>
</tr>
</tbody>
</table>

*Comparisons for Each Pair Using Student’s T*

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>p/3</td>
<td>m/2</td>
<td>3.4501</td>
<td>0.9113</td>
<td>0.0007*</td>
</tr>
<tr>
<td>p/3</td>
<td>m/1</td>
<td>2.0848</td>
<td>0.8823</td>
<td>0.0246*</td>
</tr>
<tr>
<td>p/3</td>
<td>m/3</td>
<td>1.9958</td>
<td>1.0440</td>
<td>0.0652</td>
</tr>
<tr>
<td>p/3</td>
<td>p/4</td>
<td>1.9923</td>
<td>0.9254</td>
<td>0.0392*</td>
</tr>
<tr>
<td>p/4</td>
<td>m/2</td>
<td>1.4578</td>
<td>0.6642</td>
<td>0.0358*</td>
</tr>
<tr>
<td>m/3</td>
<td>m/2</td>
<td>1.4543</td>
<td>0.8214</td>
<td>0.0865</td>
</tr>
<tr>
<td>m/1</td>
<td>m/2</td>
<td>1.3653</td>
<td>0.6027</td>
<td>0.0306*</td>
</tr>
<tr>
<td>p/4</td>
<td>m/1</td>
<td>0.0925</td>
<td>0.6239</td>
<td>0.8831</td>
</tr>
<tr>
<td>m/3</td>
<td>m/1</td>
<td>0.0890</td>
<td>0.7892</td>
<td>0.9110</td>
</tr>
<tr>
<td>p/4</td>
<td>m/3</td>
<td>0.0035</td>
<td>0.8370</td>
<td>0.9967</td>
</tr>
</tbody>
</table>

*Tests for Unequal Variance*

<table>
<thead>
<tr>
<th>Level</th>
<th>Count</th>
<th>Stand. Dev.</th>
<th>Mean to Group Mean</th>
<th>Mean to Group Median</th>
<th>F Test</th>
<th>Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>12</td>
<td>0.9807</td>
<td>0.7527</td>
<td>0.7527</td>
<td>0.7415</td>
<td>0.5710</td>
<td></td>
</tr>
<tr>
<td>m/2</td>
<td>9</td>
<td>1.4759</td>
<td>1.1139</td>
<td>1.1228</td>
<td>0.7203</td>
<td>0.5846</td>
<td></td>
</tr>
<tr>
<td>p/3</td>
<td>3</td>
<td>1.6294</td>
<td>1.2368</td>
<td>1.1986</td>
<td>0.8723</td>
<td>0.4916</td>
<td></td>
</tr>
<tr>
<td>p/4</td>
<td>8</td>
<td>1.5526</td>
<td>1.3161</td>
<td>1.3161</td>
<td>0.7415</td>
<td>0.5710</td>
<td></td>
</tr>
<tr>
<td>m/3</td>
<td>4</td>
<td>1.6052</td>
<td>1.1593</td>
<td>1.1593</td>
<td>0.5988</td>
<td>0.6635</td>
<td></td>
</tr>
</tbody>
</table>
**Table 6.** $\delta^{18}$O Statistical Analyses for D-1583, pattern B

*Analysis of Variance*

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>3</td>
<td>10.4376</td>
<td>4.4921</td>
<td>0.0273*</td>
</tr>
<tr>
<td>Error</td>
<td>11</td>
<td>2.3236</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Means for One way ANOVA*

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Stand. Dev.</th>
<th>Stand. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/l</td>
<td>4</td>
<td>21.2207</td>
<td>1.4028</td>
<td>0.7622</td>
</tr>
<tr>
<td>m/2</td>
<td>4</td>
<td>24.3623</td>
<td>1.4941</td>
<td>0.7622</td>
</tr>
<tr>
<td>p/4</td>
<td>4</td>
<td>20.7137</td>
<td>1.2500</td>
<td>0.7622</td>
</tr>
<tr>
<td>m/3</td>
<td>3</td>
<td>22.2581</td>
<td>2.0337</td>
<td>0.8801</td>
</tr>
</tbody>
</table>

*Comparisons for Each Pair Using Student's T*

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/2</td>
<td>p/4</td>
<td>3.6486</td>
<td>1.0779</td>
<td>0.0061*</td>
</tr>
<tr>
<td>m/2</td>
<td>m/l</td>
<td>3.1416</td>
<td>1.0779</td>
<td>0.0141*</td>
</tr>
<tr>
<td>m/2</td>
<td>m/3</td>
<td>2.1043</td>
<td>1.1642</td>
<td>0.0981</td>
</tr>
<tr>
<td>m/3</td>
<td>p/4</td>
<td>1.5444</td>
<td>1.1642</td>
<td>0.2115</td>
</tr>
<tr>
<td>m/3</td>
<td>m/l</td>
<td>1.0374</td>
<td>1.1642</td>
<td>0.3920</td>
</tr>
<tr>
<td>m/3</td>
<td>m/2</td>
<td>2.1043</td>
<td>1.1642</td>
<td>0.2115</td>
</tr>
<tr>
<td>m/l</td>
<td>p/4</td>
<td>0.5070</td>
<td>1.0779</td>
<td>0.6473</td>
</tr>
</tbody>
</table>

*Tests for Unequal Variance*

| Level | Count | Stand. Dev. | |Mean| to Group | |Median| to Group |
|-------|-------|-------------|----------|---------|----------|----------|
| m/l   | 4     | 1.4028      | 0.9830   | 0.9664  |
| m/2   | 4     | 1.4940      | 1.0491   | 1.0491  |
| p/4   | 4     | 1.2500      | 0.9080   | 0.7627  |
| m/3   | 3     | 2.0337      | 1.3795   | 1.9962  |

<table>
<thead>
<tr>
<th>Test</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>0.3589</td>
<td>0.7839</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>1.3225</td>
<td>0.3166</td>
</tr>
<tr>
<td>Levene</td>
<td>0.1871</td>
<td>0.9030</td>
</tr>
<tr>
<td>Bartlett</td>
<td>0.1891</td>
<td>0.9039</td>
</tr>
</tbody>
</table>

**Table 7.** $\delta^{18}$O Statistical Analyses for D-1583, pairwise ANOVA analysis

*Testing for pair-wise significance in variance*

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
<th>Unequal Variance?</th>
<th>Welch's Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/l</td>
<td>m/2</td>
<td>0.1010</td>
<td>0.7532</td>
<td>Yes*</td>
<td></td>
</tr>
<tr>
<td>m/2</td>
<td>p/4</td>
<td>0.1425</td>
<td>0.7089</td>
<td>No</td>
<td>0.7594</td>
</tr>
<tr>
<td>m/1</td>
<td>m/3</td>
<td>0.2553</td>
<td>0.6186</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>m/2</td>
<td>p/4</td>
<td>0.0214</td>
<td>0.8848</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>m/2</td>
<td>m/3</td>
<td>0.0365</td>
<td>0.8508</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>p/4</td>
<td>m/3</td>
<td>0.1072</td>
<td>0.7481</td>
<td>No</td>
<td></td>
</tr>
</tbody>
</table>

*Significance found in the O'Brien[.5], Levene, and Bartlett tests (p-value < 0.05)
# APPENDIX C

## CARBON ISOTOPE STATISTICAL ANALYSES

### Table 8. $\delta^{13}$C Statistical Analyses for ALL Locality Data Combined

#### Analysis of Variance

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>4</td>
<td>0.7553</td>
<td>1.0605</td>
<td>0.3830</td>
</tr>
<tr>
<td>Error</td>
<td>67</td>
<td>0.7122</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

#### Means for One-way ANOVA

<table>
<thead>
<tr>
<th>Group</th>
<th>Mean</th>
<th>Stand. Dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>-12.4660</td>
<td>0.5870</td>
</tr>
<tr>
<td>m/2</td>
<td>-12.0090</td>
<td>0.9863</td>
</tr>
<tr>
<td>p/3</td>
<td>-12.0660</td>
<td>1.2783</td>
</tr>
<tr>
<td>p/4</td>
<td>-12.0900</td>
<td>0.8555</td>
</tr>
<tr>
<td>m/3</td>
<td>-12.4270</td>
<td>0.8061</td>
</tr>
</tbody>
</table>

#### Comparisons for Each Pair Using Student’s T

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/2</td>
<td>m/1</td>
<td>0.4566</td>
<td>0.2616</td>
<td>0.0855</td>
</tr>
<tr>
<td>m/2</td>
<td>m/3</td>
<td>0.4175</td>
<td>0.3297</td>
<td>0.2098</td>
</tr>
<tr>
<td>p/3</td>
<td>m/1</td>
<td>0.4001</td>
<td>0.4164</td>
<td>0.3401</td>
</tr>
<tr>
<td>p/4</td>
<td>m/1</td>
<td>0.3761</td>
<td>0.2801</td>
<td>0.1839</td>
</tr>
<tr>
<td>p/3</td>
<td>m/3</td>
<td>0.3610</td>
<td>0.4622</td>
<td>0.4376</td>
</tr>
<tr>
<td>p/4</td>
<td>m/3</td>
<td>0.3370</td>
<td>0.3445</td>
<td>0.3315</td>
</tr>
<tr>
<td>m/2</td>
<td>p/4</td>
<td>0.0805</td>
<td>0.2915</td>
<td>0.7832</td>
</tr>
<tr>
<td>m/2</td>
<td>p/3</td>
<td>0.0565</td>
<td>0.4242</td>
<td>0.8944</td>
</tr>
<tr>
<td>m/3</td>
<td>m/1</td>
<td>0.0391</td>
<td>0.3197</td>
<td>0.9030</td>
</tr>
<tr>
<td>p/3</td>
<td>m/4</td>
<td>0.0240</td>
<td>0.4358</td>
<td>0.9562</td>
</tr>
</tbody>
</table>

#### Tests for Unequal Variance

<p>| Level | Count | Stand. Dev. | |Mean| to Group Mean | |Mean| to Group Median |
|-------|-------|-------------|----------------|----------------|----------------|
| m/1   | 23    | 0.5870      | 0.4902         | 0.4904         |
| m/2   | 19    | 0.9863      | 0.7625         | 0.7505         |
| p/3   | 5     | 1.2783      | 0.9192         | 0.9660         |
| p/4   | 15    | 0.8555      | 0.6800         | 0.6807         |
| m/3   | 10    | 0.8061      | 0.5758         | 0.5330         |</p>
<table>
<thead>
<tr>
<th>Test</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>2</td>
<td>0.1391</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>1</td>
<td>0.2816</td>
</tr>
<tr>
<td>Levene</td>
<td>1</td>
<td>0.2937</td>
</tr>
<tr>
<td>Bartlett</td>
<td>2</td>
<td>0.1268</td>
</tr>
</tbody>
</table>

**Table 9.** δ^13^C Statistical Analyses for D-1204

**Analysis of Variance**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>4</td>
<td>1.2190</td>
<td>2.0274</td>
<td>0.1389</td>
</tr>
<tr>
<td>Error</td>
<td>16</td>
<td>0.6013</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Means for Oneway ANOVA**

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Stand. Dev.</th>
<th>Stand. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/l</td>
<td>7</td>
<td>-12.8290</td>
<td>0.3729</td>
<td>0.2931</td>
</tr>
<tr>
<td>m/2</td>
<td>6</td>
<td>-11.7500</td>
<td>0.5505</td>
<td>0.3166</td>
</tr>
<tr>
<td>p/3</td>
<td>2</td>
<td>-12.8550</td>
<td>1.2516</td>
<td>0.5483</td>
</tr>
<tr>
<td>p/4</td>
<td>3</td>
<td>-12.0200</td>
<td>0.9215</td>
<td>0.4477</td>
</tr>
<tr>
<td>m/3</td>
<td>3</td>
<td>-12.6670</td>
<td>1.4154</td>
<td>0.4477</td>
</tr>
</tbody>
</table>

**Comparisons for Each Pair Using Student's T**

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/2</td>
<td>p/3</td>
<td>1.1050</td>
<td>0.6331</td>
<td>0.0237*</td>
</tr>
<tr>
<td>m/2</td>
<td>m/l</td>
<td>1.0786</td>
<td>0.4314</td>
<td>0.0237*</td>
</tr>
<tr>
<td>m/2</td>
<td>m/3</td>
<td>0.9167</td>
<td>0.5483</td>
<td>0.1140</td>
</tr>
<tr>
<td>p/4</td>
<td>p/3</td>
<td>0.8350</td>
<td>0.7079</td>
<td>0.2554</td>
</tr>
<tr>
<td>p/4</td>
<td>m/1</td>
<td>0.8086</td>
<td>0.5351</td>
<td>0.1503</td>
</tr>
<tr>
<td>p/4</td>
<td>m/3</td>
<td>0.6467</td>
<td>0.6331</td>
<td>0.3223</td>
</tr>
<tr>
<td>m/2</td>
<td>p/4</td>
<td>0.2700</td>
<td>0.5483</td>
<td>0.6291</td>
</tr>
<tr>
<td>m/3</td>
<td>p/3</td>
<td>0.1883</td>
<td>0.7079</td>
<td>0.7936</td>
</tr>
<tr>
<td>m/3</td>
<td>m/l</td>
<td>0.1619</td>
<td>0.5351</td>
<td>0.7661</td>
</tr>
<tr>
<td>m/1</td>
<td>p/3</td>
<td>0.0264</td>
<td>0.6217</td>
<td>0.9666</td>
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</tbody>
</table>

**Tests for Unequal Variance**

<table>
<thead>
<tr>
<th>Level</th>
<th>Count</th>
<th>Stand. Dev.</th>
<th>Mean to Group Mean</th>
<th>Mean to Group Median</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/l</td>
<td>7</td>
<td>0.3729</td>
<td>0.3020</td>
<td>0.2714</td>
</tr>
<tr>
<td>m/2</td>
<td>6</td>
<td>0.5505</td>
<td>0.4000</td>
<td>0.3833</td>
</tr>
<tr>
<td>p/3</td>
<td>2</td>
<td>1.2516</td>
<td>0.8850</td>
<td>0.8850</td>
</tr>
<tr>
<td>p/4</td>
<td>3</td>
<td>0.9215</td>
<td>0.6333</td>
<td>0.8900</td>
</tr>
<tr>
<td>m/3</td>
<td>3</td>
<td>1.4154</td>
<td>1.0889</td>
<td>0.8667</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Test</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>2</td>
<td>0.1087</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>1</td>
<td>0.3002</td>
</tr>
<tr>
<td>Levene</td>
<td>4</td>
<td>0.0201*</td>
</tr>
<tr>
<td>Bartlett</td>
<td>2</td>
<td>0.1444</td>
</tr>
<tr>
<td>Welch's Test</td>
<td>2.9153</td>
<td>0.1644</td>
</tr>
</tbody>
</table>
Table 10. $\delta^{13}$C Statistical Analyses for D-1583

**Analysis of Variance**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>4</td>
<td>0.4320</td>
<td>0.5872</td>
<td>0.6736</td>
</tr>
<tr>
<td>Error</td>
<td>47</td>
<td>0.7358</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Means for Oneway ANOVA**

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Stand. Dev.</th>
<th>Stand. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>16</td>
<td>-12.3080</td>
<td>0.6013</td>
<td>0.2145</td>
</tr>
<tr>
<td>m/2</td>
<td>13</td>
<td>-12.1290</td>
<td>1.1330</td>
<td>0.2379</td>
</tr>
<tr>
<td>p/3</td>
<td>3</td>
<td>-11.5400</td>
<td>1.2031</td>
<td>0.4952</td>
</tr>
<tr>
<td>p/4</td>
<td>12</td>
<td>-12.1080</td>
<td>0.8805</td>
<td>0.2476</td>
</tr>
<tr>
<td>m/3</td>
<td>7</td>
<td>-12.3240</td>
<td>0.5156</td>
<td>0.3242</td>
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</table>

**Comparisons for Each Pair Using Student's T**

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>p/3</td>
<td>m/3</td>
<td>0.7843</td>
<td>0.5919</td>
<td>0.1917</td>
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<tr>
<td>p/3</td>
<td>m/1</td>
<td>0.7675</td>
<td>0.5397</td>
<td>0.1617</td>
</tr>
<tr>
<td>p/3</td>
<td>m/2</td>
<td>0.5892</td>
<td>0.5494</td>
<td>0.2891</td>
</tr>
<tr>
<td>p/3</td>
<td>p/4</td>
<td>0.5675</td>
<td>0.5537</td>
<td>0.3108</td>
</tr>
<tr>
<td>p/4</td>
<td>m/3</td>
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<td>0.4080</td>
<td>0.5977</td>
</tr>
<tr>
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<td>m/1</td>
<td>0.2000</td>
<td>0.3276</td>
<td>0.5445</td>
</tr>
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<td>m/2</td>
<td>m/3</td>
<td>0.1951</td>
<td>0.4021</td>
<td>0.6299</td>
</tr>
<tr>
<td>m/2</td>
<td>m/1</td>
<td>0.1783</td>
<td>0.3203</td>
<td>0.5805</td>
</tr>
<tr>
<td>p/4</td>
<td>m/2</td>
<td>0.0217</td>
<td>0.3434</td>
<td>0.9498</td>
</tr>
<tr>
<td>m/1</td>
<td>m/3</td>
<td>0.0168</td>
<td>0.3887</td>
<td>0.9657</td>
</tr>
</tbody>
</table>

**Tests for Unequal Variance**

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<th>Median to Group</th>
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</thead>
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<td>0.6013</td>
<td>0.4847</td>
<td>0.4700</td>
</tr>
<tr>
<td>m/2</td>
<td>13</td>
<td>1.1330</td>
<td>0.9053</td>
<td>0.9131</td>
</tr>
<tr>
<td>p/3</td>
<td>3</td>
<td>1.2031</td>
<td>0.8330</td>
<td>1.1500</td>
</tr>
<tr>
<td>p/4</td>
<td>12</td>
<td>0.8805</td>
<td>0.6958</td>
<td>0.6958</td>
</tr>
<tr>
<td>m/3</td>
<td>7</td>
<td>0.5156</td>
<td>0.3620</td>
<td>0.3571</td>
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</table>

<table>
<thead>
<tr>
<th>Test</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>2</td>
<td>0.0884</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>3</td>
<td>0.0241*</td>
</tr>
<tr>
<td>Levene</td>
<td>2</td>
<td>0.0891</td>
</tr>
<tr>
<td>Bartlett</td>
<td>2</td>
<td>0.1075</td>
</tr>
<tr>
<td>Welch's Test</td>
<td>0.3807</td>
<td>0.8180</td>
</tr>
</tbody>
</table>

74
Table 11. $\delta^{13}$C Statistical Analyses for D-1583, pattern A

**Analysis of Variance**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>4</td>
<td>0.8449</td>
<td>1.2273</td>
<td>0.3195</td>
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<tr>
<td>Error</td>
<td>31</td>
<td>0.6884</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Means for One-way ANOVA**

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Stand. Dev.</th>
<th>Stand. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>12</td>
<td>-12.1280</td>
<td>0.4710</td>
<td>0.2395</td>
</tr>
<tr>
<td>m/2</td>
<td>9</td>
<td>-12.5180</td>
<td>1.1654</td>
<td>0.2766</td>
</tr>
<tr>
<td>p/3</td>
<td>3</td>
<td>-11.5400</td>
<td>1.2031</td>
<td>0.4790</td>
</tr>
<tr>
<td>p/4</td>
<td>8</td>
<td>-11.7740</td>
<td>0.8296</td>
<td>0.2934</td>
</tr>
<tr>
<td>m/3</td>
<td>4</td>
<td>-12.0450</td>
<td>0.3279</td>
<td>0.4149</td>
</tr>
</tbody>
</table>

**Comparisons for Each Pair Using Student's T**

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>p/3</td>
<td>m/2</td>
<td>0.7440</td>
<td>0.5531</td>
<td>0.0745</td>
</tr>
<tr>
<td>p/4</td>
<td>m/2</td>
<td>0.7440</td>
<td>0.5531</td>
<td>0.0745</td>
</tr>
<tr>
<td>p/3</td>
<td>m/1</td>
<td>0.5875</td>
<td>0.5356</td>
<td>0.2811</td>
</tr>
<tr>
<td>p/3</td>
<td>m/3</td>
<td>0.5050</td>
<td>0.6337</td>
<td>0.4316</td>
</tr>
<tr>
<td>m/3</td>
<td>m/2</td>
<td>0.4728</td>
<td>0.4986</td>
<td>0.3503</td>
</tr>
<tr>
<td>m/1</td>
<td>m/2</td>
<td>0.3903</td>
<td>0.3659</td>
<td>0.2943</td>
</tr>
<tr>
<td>p/4</td>
<td>m/1</td>
<td>0.3538</td>
<td>0.3787</td>
<td>0.3575</td>
</tr>
<tr>
<td>p/4</td>
<td>m/3</td>
<td>0.2713</td>
<td>0.5081</td>
<td>0.5972</td>
</tr>
<tr>
<td>p/3</td>
<td>p/4</td>
<td>0.2338</td>
<td>0.5617</td>
<td>0.6802</td>
</tr>
<tr>
<td>m/3</td>
<td>m/1</td>
<td>0.0825</td>
<td>0.4790</td>
<td>0.8644</td>
</tr>
</tbody>
</table>

**Tests for Unequal Variance**

| Level | Count | Stand. Dev. | |Mean| to Group Mean | |Mean| to Group Median |
|-------|-------|-------------|--------|----------------|--------|
| m/1   | 12    | 0.4710      | 0.3613 | 0.3608         |
| m/2   | 9     | 1.1654      | 0.8536 | 0.8489         |
| p/3   | 3     | 1.2031      | 0.8333 | 1.1500         |
| p/4   | 8     | 0.8296      | 0.6238 | 0.6238         |
| m/3   | 4     | 0.3279      | 0.2750 | 0.2750         |

<table>
<thead>
<tr>
<th>Test</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>1</td>
<td>0.2358</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>3</td>
<td><strong>0.0475</strong>*</td>
</tr>
<tr>
<td>Levene</td>
<td>2</td>
<td>0.1476</td>
</tr>
<tr>
<td>Bartlett</td>
<td>3</td>
<td><strong>0.0383</strong>*</td>
</tr>
<tr>
<td>Welch's Test</td>
<td>0.6415</td>
<td>0.6462</td>
</tr>
</tbody>
</table>
Table 12. \( ^{\text{\$13}}C \) Statistical Analyses for D-1583, pattern B

**Analysis of Variance**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Proh &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>3</td>
<td>2.2870</td>
<td>8.0298</td>
<td>0.0041*</td>
</tr>
<tr>
<td>Error</td>
<td>11</td>
<td>0.2848</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Means for Oneway ANOVA**

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Stand. Dev.</th>
<th>Stand. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>4</td>
<td>-12.8480</td>
<td>0.6900</td>
<td>0.2668</td>
</tr>
<tr>
<td>m/2</td>
<td>4</td>
<td>-11.2550</td>
<td>0.2022</td>
<td>0.2668</td>
</tr>
<tr>
<td>p/4</td>
<td>4</td>
<td>-12.7750</td>
<td>0.5880</td>
<td>0.2668</td>
</tr>
<tr>
<td>m/3</td>
<td>3</td>
<td>-12.6970</td>
<td>0.5218</td>
<td>0.3081</td>
</tr>
</tbody>
</table>

**Comparisons for Each Pair Using Student’s T**

<table>
<thead>
<tr>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/2</td>
<td>1.5925</td>
<td>0.3774</td>
<td>0.0014*</td>
</tr>
<tr>
<td>m/2</td>
<td>1.5200</td>
<td>0.3774</td>
<td>0.0020*</td>
</tr>
<tr>
<td>m/2</td>
<td>1.4417</td>
<td>0.4076</td>
<td>0.0047*</td>
</tr>
<tr>
<td>m/3</td>
<td>0.1508</td>
<td>0.4076</td>
<td>0.7184</td>
</tr>
<tr>
<td>m/3</td>
<td>0.0783</td>
<td>0.4076</td>
<td>0.8511</td>
</tr>
<tr>
<td>p/4</td>
<td>0.0725</td>
<td>0.3774</td>
<td>0.8511</td>
</tr>
</tbody>
</table>

**Tests for Unequal Variance**

| Level | Count | Stand. Dev. | |Mean| to Group Mean | |Mean| to Group Median |
|-------|-------|-------------|----------------|----------------|-----------------|
| m/1   | 4     | 0.6900      | 0.5275         | 0.5275         |
| m/2   | 4     | 0.2022      | 0.1450         | 0.1450         |
| p/4   | 4     | 0.5880      | 0.4850         | 0.4850         |
| m/3   | 3     | 0.5218      | 0.3756         | 0.4667         |

<table>
<thead>
<tr>
<th>Test</th>
<th>Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>1</td>
<td>0.4513</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>2</td>
<td>0.1466</td>
</tr>
<tr>
<td>Levene</td>
<td>2</td>
<td>0.1388</td>
</tr>
<tr>
<td>Bartlett</td>
<td>1</td>
<td>0.3510</td>
</tr>
</tbody>
</table>
APPENDIX D

COMPARING ALTERED AND PRISTINE SAMPLES

Table 13. \( ^{18}O \) statistical analyses for D-1204, altered samples vs. pristine samples

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>( F ) Ratio</th>
<th>( \text{Prob} &gt; F )</th>
</tr>
</thead>
<tbody>
<tr>
<td>condition</td>
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<td>13.4538</td>
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<td>Error</td>
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</table>

<table>
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<th>Mean</th>
<th>Std Dev</th>
<th>Std Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>altered</td>
<td>6</td>
<td>19.8282</td>
<td>2.82599</td>
<td>0.87641</td>
</tr>
<tr>
<td>pristine</td>
<td>19</td>
<td>21.5459</td>
<td>1.91579</td>
<td>0.4925</td>
</tr>
</tbody>
</table>

Table 14. \( ^{13}C \) statistical analyses for D-1204, altered samples vs. pristine samples

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>( F ) Ratio</th>
<th>( \text{Prob} &gt; F )</th>
</tr>
</thead>
<tbody>
<tr>
<td>condition</td>
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<td>0.654518</td>
<td>0.9503</td>
<td>0.3398</td>
</tr>
<tr>
<td>Error</td>
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<td>0.688747</td>
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<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Std Dev</th>
<th>Std Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>altered</td>
<td>6</td>
<td>-12.778</td>
<td>0.53697</td>
<td>0.33881</td>
</tr>
<tr>
<td>pristine</td>
<td>19</td>
<td>-12.399</td>
<td>0.894411</td>
<td>0.19039</td>
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</table>
Table 15. δ¹⁸O Statistical Analyses for D-1204, including altered & questionable samples

**Analysis of Variance**

<table>
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<tr>
<th>Source</th>
<th>DF</th>
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<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>5</td>
<td>10.4376</td>
<td>3.2455</td>
<td>0.0276*</td>
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<td>2.3236</td>
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<td></td>
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</table>

**Means for One-way ANOVA**

<table>
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<th>Stand. Dev.</th>
<th>Stand. Error</th>
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<tbody>
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<tr>
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<td>7</td>
<td>21.4082</td>
<td>2.28118</td>
<td>0.696</td>
</tr>
<tr>
<td>p/3</td>
<td>2</td>
<td>21.8178</td>
<td>2.01519</td>
<td>1.3021</td>
</tr>
<tr>
<td>p/4</td>
<td>3</td>
<td>23.7716</td>
<td>2.19081</td>
<td>1.0631</td>
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<tr>
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<td>18.68</td>
<td>1.82816</td>
<td>0.8235</td>
</tr>
</tbody>
</table>

**Comparisons for Each Pair Using Student’s T**

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>p/4</td>
<td>m/3</td>
<td>5.091639</td>
<td>1.344775</td>
<td>0.0012*</td>
</tr>
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<td>m/3</td>
<td>3.137805</td>
<td>1.540633</td>
<td>0.0559</td>
</tr>
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<td>m/3</td>
<td>2.795464</td>
<td>1.078218</td>
<td>0.0179*</td>
</tr>
<tr>
<td>m/2</td>
<td>m/3</td>
<td>2.728217</td>
<td>1.078218</td>
<td>0.0204*</td>
</tr>
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<td>p/4</td>
<td>m/2</td>
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<td>1.270693</td>
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<td>m/2</td>
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<td>1.270693</td>
<td>0.0866</td>
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<tr>
<td>p/4</td>
<td>p/3</td>
<td>1.953835</td>
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<td>0.2595</td>
</tr>
<tr>
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<td>m/2</td>
<td>0.409588</td>
<td>1.476411</td>
<td>0.7845</td>
</tr>
<tr>
<td>p/3</td>
<td>m/2</td>
<td>0.342341</td>
<td>1.476411</td>
<td>0.8191</td>
</tr>
<tr>
<td>m/1</td>
<td>m/2</td>
<td>0.067246</td>
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<td>0.9462</td>
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</table>

**Tests for Unequal Variance**

<table>
<thead>
<tr>
<th>Level</th>
<th>Count</th>
<th>Stand. Dev.</th>
<th>[Mean] to Group Mean</th>
<th>[Mean] to Group Median</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>7</td>
<td>1.014337</td>
<td>0.695851</td>
<td>0.706897</td>
</tr>
<tr>
<td>m/2</td>
<td>7</td>
<td>2.281179</td>
<td>1.664168</td>
<td>1.523614</td>
</tr>
<tr>
<td>p/3</td>
<td>2</td>
<td>2.01519</td>
<td>1.424955</td>
<td>1.424955</td>
</tr>
<tr>
<td>p/4</td>
<td>3</td>
<td>2.190813</td>
<td>1.686464</td>
<td>1.276676</td>
</tr>
<tr>
<td>m/3</td>
<td>5</td>
<td>1.82816</td>
<td>1.130544</td>
<td>1.154016</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Test</th>
<th>Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>0.5813</td>
<td>0.6349</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>0.3403</td>
<td>0.8474</td>
</tr>
<tr>
<td>Levene</td>
<td>0.8496</td>
<td>0.5114</td>
</tr>
<tr>
<td>Bartlett</td>
<td>0.8057</td>
<td>0.5213</td>
</tr>
</tbody>
</table>
Table 16. $\delta^{13}$C Statistical Analyses for D-1204, including altered & questionable samples

### Analysis of Variance

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>5</td>
<td>0.9589</td>
<td>1.5570</td>
<td>0.2199</td>
</tr>
<tr>
<td>Error</td>
<td>19</td>
<td>0.6159</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Means for Oneway ANOVA

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Stand. Dev.</th>
<th>Stand. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>7</td>
<td>-12.8290</td>
<td>0.3729</td>
<td>0.2966</td>
</tr>
<tr>
<td>m/2</td>
<td>7</td>
<td>-11.9710</td>
<td>0.7718</td>
<td>0.2966</td>
</tr>
<tr>
<td>p/3</td>
<td>2</td>
<td>-12.8550</td>
<td>1.2516</td>
<td>0.5549</td>
</tr>
<tr>
<td>p/4</td>
<td>3</td>
<td>-12.0200</td>
<td>0.9215</td>
<td>0.4531</td>
</tr>
<tr>
<td>m/3</td>
<td>5</td>
<td>-12.6800</td>
<td>1.0035</td>
<td>0.3510</td>
</tr>
</tbody>
</table>

### Comparisons for Each Pair Using Student's T

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/2</td>
<td>p/3</td>
<td>0.8836</td>
<td>0.6292</td>
<td>0.1764</td>
</tr>
<tr>
<td>m/2</td>
<td>m/1</td>
<td>0.8571</td>
<td>0.4195</td>
<td>0.0551</td>
</tr>
<tr>
<td>p/4</td>
<td>p/3</td>
<td>0.8350</td>
<td>0.7164</td>
<td>0.2582</td>
</tr>
<tr>
<td>p/4</td>
<td>m/1</td>
<td>0.8086</td>
<td>0.5415</td>
<td>0.1518</td>
</tr>
<tr>
<td>m/2</td>
<td>m/3</td>
<td>0.7086</td>
<td>0.4595</td>
<td>0.1396</td>
</tr>
<tr>
<td>p/4</td>
<td>m/3</td>
<td>0.6600</td>
<td>0.5731</td>
<td>0.2638</td>
</tr>
<tr>
<td>m/3</td>
<td>p/3</td>
<td>0.1750</td>
<td>0.6566</td>
<td>0.7927</td>
</tr>
<tr>
<td>m/3</td>
<td>m/1</td>
<td>0.1486</td>
<td>0.4595</td>
<td>0.7500</td>
</tr>
<tr>
<td>m/2</td>
<td>p/4</td>
<td>0.0486</td>
<td>0.5415</td>
<td>0.9295</td>
</tr>
<tr>
<td>m/1</td>
<td>p/3</td>
<td>0.0264</td>
<td>0.6292</td>
<td>0.9669</td>
</tr>
</tbody>
</table>

### Tests for Unequal Variance

<table>
<thead>
<tr>
<th>Level</th>
<th>Count</th>
<th>Stand. Dev.</th>
<th>Mean to Group Mean</th>
<th>Mean to Group Median</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>7</td>
<td>0.3729</td>
<td>0.3020</td>
<td>0.2714</td>
</tr>
<tr>
<td>m/2</td>
<td>7</td>
<td>0.7718</td>
<td>0.5673</td>
<td>0.5429</td>
</tr>
<tr>
<td>p/3</td>
<td>2</td>
<td>1.2516</td>
<td>0.8850</td>
<td>0.8850</td>
</tr>
<tr>
<td>p/4</td>
<td>3</td>
<td>0.9215</td>
<td>0.6333</td>
<td>0.8900</td>
</tr>
<tr>
<td>m/3</td>
<td>5</td>
<td>1.0035</td>
<td>0.6960</td>
<td>0.7200</td>
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</table>

<table>
<thead>
<tr>
<th>Test</th>
<th>Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[5]</td>
<td>1</td>
<td>0.4534</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>2</td>
<td>0.2237</td>
</tr>
<tr>
<td>Levene</td>
<td>1</td>
<td>0.4174</td>
</tr>
<tr>
<td>Bartlett</td>
<td>1</td>
<td>0.3109</td>
</tr>
</tbody>
</table>
Table 17. $\delta^{18}$O statistical analyses for D-1583, altered samples vs. pristine samples

**Analysis of Variance**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>condition</td>
<td>1</td>
<td>0.57898</td>
<td>0.206</td>
<td>0.6515</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td>2.81031</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Means for One way Anova**

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Std Dev</th>
<th>Std Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>altered</td>
<td>12</td>
<td>22.4418</td>
<td>1.58186</td>
<td>0.48393</td>
</tr>
<tr>
<td>pristine</td>
<td>50</td>
<td>22.1972</td>
<td>1.6969</td>
<td>0.23708</td>
</tr>
</tbody>
</table>

Table 18. $\delta^{13}$C statistical analyses for D-1583, altered samples vs. pristine samples

**Analysis of Variance**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>condition</td>
<td>1</td>
<td>0.654518</td>
<td>0.9503</td>
<td>0.3398</td>
</tr>
<tr>
<td>Error</td>
<td>23</td>
<td>0.688747</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Means for One way Anova**

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Std Dev</th>
<th>Std Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>altered</td>
<td>6</td>
<td>-12.778</td>
<td>0.53697</td>
<td>0.33881</td>
</tr>
<tr>
<td>pristine</td>
<td>19</td>
<td>-12.399</td>
<td>0.894411</td>
<td>0.19039</td>
</tr>
</tbody>
</table>
### Table 19. δ¹⁸O Statistical Analyses for D-1583, including altered & questionable samples

#### Analysis of Variance

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>4</td>
<td>1.29042</td>
<td>0.4477</td>
<td>0.7736</td>
</tr>
<tr>
<td>Error</td>
<td>58</td>
<td>2.88223</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

#### Means for Oneway ANOVA

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Stand. Dev.</th>
<th>Stand. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>19</td>
<td>22.2481</td>
<td>1.3186</td>
<td>0.38948</td>
</tr>
<tr>
<td>m/2</td>
<td>17</td>
<td>22.0119</td>
<td>2.0522</td>
<td>0.41176</td>
</tr>
<tr>
<td>p/3</td>
<td>5</td>
<td>23.0694</td>
<td>2.21613</td>
<td>0.75924</td>
</tr>
<tr>
<td>p/4</td>
<td>14</td>
<td>22.0173</td>
<td>1.58533</td>
<td>0.45373</td>
</tr>
<tr>
<td>m/3</td>
<td>8</td>
<td>22.3894</td>
<td>1.51989</td>
<td>0.60023</td>
</tr>
</tbody>
</table>

#### Comparisons for Each Pair Using Student's T

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>p/3</td>
<td>m/2</td>
<td>1.057414</td>
<td>0.8637061</td>
<td>0.2258</td>
</tr>
<tr>
<td>p/3</td>
<td>p/4</td>
<td>1.052031</td>
<td>0.8844879</td>
<td>0.2391</td>
</tr>
<tr>
<td>p/3</td>
<td>m/1</td>
<td>0.821261</td>
<td>0.8533121</td>
<td>0.3398</td>
</tr>
<tr>
<td>p/3</td>
<td>m/3</td>
<td>0.679952</td>
<td>0.967845</td>
<td>0.4852</td>
</tr>
<tr>
<td>m/3</td>
<td>m/2</td>
<td>0.377462</td>
<td>0.7278882</td>
<td>0.606</td>
</tr>
<tr>
<td>m/3</td>
<td>p/4</td>
<td>0.372079</td>
<td>0.7524306</td>
<td>0.6228</td>
</tr>
<tr>
<td>m/1</td>
<td>m/2</td>
<td>0.236153</td>
<td>0.5667795</td>
<td>0.6785</td>
</tr>
<tr>
<td>m/1</td>
<td>p/4</td>
<td>0.23077</td>
<td>0.5979712</td>
<td>0.701</td>
</tr>
<tr>
<td>m/3</td>
<td>m/1</td>
<td>0.141309</td>
<td>0.715524</td>
<td>0.8441</td>
</tr>
<tr>
<td>p/4</td>
<td>m/2</td>
<td>0.005383</td>
<td>0.6127121</td>
<td>0.993</td>
</tr>
</tbody>
</table>

#### Tests for Unequal Variance

| Level | Count | Stand. Dev. | |Mean| to Group | Median |
|-------|-------|-------------| | | | |
| m/1   | 19    | 1.318598    | 1.054221 | 1.060862 |
| m/2   | 17    | 2.052203    | 1.665794 | 1.627852 |
| p/3   | 5     | 2.216129    | 1.805435 | 1.846497 |
| p/4   | 14    | 1.853332    | 1.365589 | 1.347903 |
| m/3   | 8     | 1.519889    | 1.137692 | 1.137692 |

<table>
<thead>
<tr>
<th>Test</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>1.7948</td>
<td>0.1422</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>1.214</td>
<td>0.3147</td>
</tr>
<tr>
<td>Levere</td>
<td>1.4946</td>
<td>0.2157</td>
</tr>
<tr>
<td>Bartlett</td>
<td>1.0089</td>
<td>0.4012</td>
</tr>
</tbody>
</table>
Table 20. $\delta^{13}$C Statistical Analyses for D-1583, including altered & questionable samples

**Analysis of Variance**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob $&gt; F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Position</td>
<td>4</td>
<td>0.4546</td>
<td>0.6420</td>
<td>0.6347</td>
</tr>
<tr>
<td>Error</td>
<td>58</td>
<td>0.7081</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Means for One-Way ANOVA**

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>Stand. Dev.</th>
<th>Stand. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>19</td>
<td>-12.3720</td>
<td>0.6515</td>
<td>0.1931</td>
</tr>
<tr>
<td>m/2</td>
<td>17</td>
<td>-12.2110</td>
<td>1.0773</td>
<td>0.2041</td>
</tr>
<tr>
<td>p/3</td>
<td>5</td>
<td>-11.8220</td>
<td>0.9343</td>
<td>0.3763</td>
</tr>
<tr>
<td>p/4</td>
<td>14</td>
<td>-12.0230</td>
<td>0.8669</td>
<td>0.2249</td>
</tr>
<tr>
<td>m/3</td>
<td>8</td>
<td>-12.3140</td>
<td>0.4783</td>
<td>0.2975</td>
</tr>
</tbody>
</table>

**Comparisons for Each Pair Using Student's T**

<table>
<thead>
<tr>
<th>Group</th>
<th>Group</th>
<th>Difference</th>
<th>Std. Err. Diff.</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>p/3</td>
<td>m/1</td>
<td>0.5496</td>
<td>0.4230</td>
<td>0.1990</td>
</tr>
<tr>
<td>p/3</td>
<td>m/3</td>
<td>0.4918</td>
<td>0.4797</td>
<td>0.3096</td>
</tr>
<tr>
<td>p/3</td>
<td>m/2</td>
<td>0.3886</td>
<td>0.4281</td>
<td>0.3678</td>
</tr>
<tr>
<td>p/4</td>
<td>m/1</td>
<td>0.3487</td>
<td>0.2964</td>
<td>0.2442</td>
</tr>
<tr>
<td>p/4</td>
<td>m/3</td>
<td>0.2909</td>
<td>0.3730</td>
<td>0.4386</td>
</tr>
<tr>
<td>p/3</td>
<td>p/4</td>
<td>0.2009</td>
<td>0.4384</td>
<td>0.6486</td>
</tr>
<tr>
<td>p/4</td>
<td>m/2</td>
<td>0.1877</td>
<td>0.3037</td>
<td>0.5389</td>
</tr>
<tr>
<td>m/2</td>
<td>m/1</td>
<td>0.1610</td>
<td>0.2809</td>
<td>0.5688</td>
</tr>
<tr>
<td>m/2</td>
<td>m/3</td>
<td>0.1032</td>
<td>0.3608</td>
<td>0.7759</td>
</tr>
<tr>
<td>m/3</td>
<td>m/1</td>
<td>0.0578</td>
<td>0.3547</td>
<td>0.8710</td>
</tr>
</tbody>
</table>

**Tests for Unequal Variance**

<table>
<thead>
<tr>
<th>Level</th>
<th>Count</th>
<th>Stand. Dev.</th>
<th>Mean to Group Mean</th>
<th>Mean to Group Median</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/1</td>
<td>19</td>
<td>0.6515</td>
<td>0.5113</td>
<td>0.4942</td>
</tr>
<tr>
<td>m/2</td>
<td>17</td>
<td>1.0773</td>
<td>0.8523</td>
<td>0.8512</td>
</tr>
<tr>
<td>p/3</td>
<td>5</td>
<td>0.9343</td>
<td>0.6856</td>
<td>0.6100</td>
</tr>
<tr>
<td>p/4</td>
<td>14</td>
<td>0.8669</td>
<td>0.6867</td>
<td>0.6786</td>
</tr>
<tr>
<td>m/3</td>
<td>8</td>
<td>0.4783</td>
<td>0.3247</td>
<td>0.3113</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Test</th>
<th>Ratio</th>
<th>Prob $&gt; F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>2</td>
<td>0.1394</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>2</td>
<td>0.1481</td>
</tr>
<tr>
<td>Levene</td>
<td>2</td>
<td>0.1083</td>
</tr>
<tr>
<td>Bartlett</td>
<td>2</td>
<td>0.1226</td>
</tr>
</tbody>
</table>
APPENDIX E

DISTRIBUTION OF DIFFERENCES BETWEEN M/1 AND M/2 TEETH

Table 21. List of m/1s and m/2s from same jaw with associated isotopic differences

<table>
<thead>
<tr>
<th>Locality</th>
<th>Pattern</th>
<th>Sample</th>
<th>Tooth</th>
<th>$\delta^{18}O$ (SMOW)</th>
<th>m/1 - m/2</th>
</tr>
</thead>
<tbody>
<tr>
<td>D-1204</td>
<td>Pattern 2</td>
<td>12A</td>
<td>L. M/1</td>
<td>21.65854482</td>
<td>-1.30615231</td>
</tr>
<tr>
<td>D-1204</td>
<td>Pattern 2</td>
<td>12B</td>
<td>L. M/2</td>
<td>22.9649713</td>
<td></td>
</tr>
<tr>
<td>D-1204</td>
<td>Pattern 2</td>
<td>14A</td>
<td>R. M/1</td>
<td>21.33682889</td>
<td>-2.35752286</td>
</tr>
<tr>
<td>D-1204</td>
<td>Pattern 2</td>
<td>14B</td>
<td>R. M/2</td>
<td>23.69435175</td>
<td></td>
</tr>
<tr>
<td>D-1204</td>
<td>Pattern 2</td>
<td>15A</td>
<td>R. M/1</td>
<td>21.91894041</td>
<td>0.06995702</td>
</tr>
<tr>
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<td>Pattern 2</td>
<td>15B</td>
<td>R. M/2</td>
<td>21.84898339</td>
<td></td>
</tr>
<tr>
<td>D-1204</td>
<td>Pattern 2</td>
<td>18A</td>
<td>R. M/1</td>
<td>21.19373552</td>
<td>-0.54244938</td>
</tr>
<tr>
<td>D-1204</td>
<td>Pattern 2</td>
<td>18B</td>
<td>R. M/2</td>
<td>21.7361849</td>
<td></td>
</tr>
<tr>
<td>D-1583</td>
<td>Pattern 1</td>
<td>45C</td>
<td>L. M/1</td>
<td>22.8131812</td>
<td>1.94556192</td>
</tr>
<tr>
<td>D-1583</td>
<td>Pattern 1</td>
<td>45D</td>
<td>L. M/2</td>
<td>20.86761928</td>
<td></td>
</tr>
<tr>
<td>D-1583</td>
<td>Pattern 1</td>
<td>48A</td>
<td>L. M/1</td>
<td>22.73882495</td>
<td>1.12857942</td>
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Table 22. Distribution statistics for m/1 - m/2 tooth positions

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<th>Upper 95%</th>
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<tr>
<td>Location</td>
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APPENDIX F

COMPARING δ13C TO δ18O VALUES, BOTH PATTERNS

Table 23. Comparing δ13C to δ18O values, Pattern A

Linear Fit
δ13C = -20.33614 + 0.3719145*δ18O

Summary of Fit
RSquare 0.4877
RSquare Adj 0.4726
Root Mean Square Error 0.6103
Mean of Response -12.0883
Observations (or Sum Wgts) 36

Analysis of Variance

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<th>DF</th>
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<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
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<td>24.7203</td>
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Table 24. Comparing δ13C to δ18O values, Pattern B

Linear Fit
δ13C = -18.59342 + 0.2846038*δ18O

Summary of Fit
RSquare 0.4176
RSquare Adj 0.3994
Root Mean Square Error 0.6664
Mean of Response -12.3879
Observations (or Sum Wgts) 34

Analysis of Variance

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APPENDIX G

MODERN MAMMAL BODY WEIGHTS AND TOOTH FORMATION TIMING

Table 25. Body weight determination of D-1583 *Hyracotherium aemulor* specimens

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*Mean Weight (kg)*

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*Mean Weight (kg)*

7.46  23.10
Table 26. List of Modern Mammals and associated body weights & age at final tooth eruption

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<th>Common Name</th>
<th>Genus</th>
<th>Species</th>
<th>Max Lifespan (years)</th>
<th>Adult Body Weight (kg)</th>
<th>Final Tooth Eruption (yrs)</th>
<th>Log_{10} Body Weight</th>
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<td>Capra</td>
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<td>20.80</td>
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</table>

*All maximum lifespans were collected from the Animal Ageing and Longevity Database (http://genomics.senescence.info/species/), and all tooth formation timing was collected from Hillson (1986)

Table 27. Comparing body weights and age at final tooth eruption

**Linear Fit**

Final Tooth Eruption = 0.0471856 + 1.3952666*LogBodyWeight

**Summary of Fit**

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<td>13</td>
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**Analysis of Variance**

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<tr>
<th>Source</th>
<th>DF</th>
<th>Sum of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>Prob &gt; F</th>
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<tr>
<td>Model</td>
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<td>11.095204</td>
<td>11.0952</td>
<td>15.3495</td>
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<td>Error</td>
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<td>0.7228</td>
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<td>C. Total</td>
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<td>19.046431</td>
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