

PALEOECOLOGY OF FOREST ENVIRONMENTS THROUGH TIME: EVIDENCE FROM
STABLE ISOTOPES OF MAMMALIAN HERBIVORES IN THE NEW WORLD

By

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To my family, especially my husband and daughter, for their unending support and constant source of inspiration that have enabled me to pursue my dreams

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Understanding the paleoecology of forest environments is critical to comprehending the context of mammalian evolution, particularly of forest-dwelling taxa. Significant work has helped clarify the timing and consequences of the evolution of grassland biomes in North America. In contrast, the paleoecology of forest environments during the late Cenozoic in southeastern North America requires further study. Therefore, my dissertation aims to understand the ecology of forest environments using stable isotopes of mammalian herbivores.

With a focus on forest-dwelling tapirs and their ancestors, in the first part I document carbon and oxygen isotope variation in extant tapirs, at the individual, population, and species level. Extant tapirs are also compared across latitudes and in areas with varying temperature and/or precipitation regimes to understand how tapirs track carbon and oxygen isotopes. These results demonstrate the conservative dietary niches of extant tapirs and the relationship between decreased drinking behavior and increased local precipitation. These data are informative to conservationists managing tapir habitats and constrain paleoecological interpretations of the southeastern fossil sites examined. In the second part, the tapir-dominated Gray Fossil Site in eastern Tennessee provides rare insight into the ecological dynamics occurring during the late Neogene, a time of dramatic global change. Isotopic evidence clarifies ecological niches,

relative seasonality, and suggests that the Appalachians may have served as a forest refugium between approximately 4.5 and 7 million years ago. In the third part, extinct tapirs and tapiroids are determined to be indicators of forest environments over the past 55 million years, based on craniodental morphology and carbon isotopes, and used to understand how forest distributions in North America have changed over time. Specifically, declines in tapiroid latitudinal ranges during the Oligocene are consistent with climatic cooling of $\sim 8^{\circ}\text{C}$ while their recent retreat (within the last $\sim 10,000$ years) to only southern distributions below 21°N indicates human interference. Collectively, my dissertation research helps elucidate how forests and their mammalian inhabitants have changed over time during the Cenozoic in the New World.

CHAPTER 1 INTRODUCTION

Current global climate change has been documented to alter the composition and dynamics of mammalian communities and their environments (Walther et al., 2002; Parmesan and Yohe, 2003; Post and Forchhammer, 2004). Documenting past climate and environmental change is critical to understanding the context of mammalian evolution. Significant work has focused on clarifying the evolution of grassland ecosystems and their mammalian inhabitants (Wang et al., 1994, Cerling et al., 1997; Feranec and MacFadden, 2000; Koch et al., 2004; Retallack, 2001; Stromberg, 2005), however the paleoecology of forest ecosystems are less understood. Forest environments currently receive a significant amount of conservation attention and contain the majority of designated “hotspots” due to high species richness, threatened/endangered species listings, and/or high endemism (Myers et al., 2000; Orme et al., 2005). Their presumed evolutionary importance as incubators of biodiversity is due in part to their potential role as refugia for taxa during periods of climate change (Haffer, 1969; Haffer and Prance, 2001). Thus, it is critical to understand the ancient ecology of forest environments and how their distributions have changed over time.

Mammalian taxa hold clues to their past environments in their teeth. Traditionally, the morphological characters including relative size and shape of teeth are used to infer the diets of extinct mammals based on modern mammalian analogues (Solounias and Moelleken, 1993; MacFadden and Shockey, 1997; Mendoza et al., 2002). Ever since the classic work of Kowalevsky (1873), teeth that are taller than they are wide (i.e. hypsodont) are thought to indicate the consumption of grass (Janis, 1988; MacFadden, 1992). This is because grass contains phytoliths that wear down tooth enamel over time (Baker et al., 1959), thus high crowned teeth can withstand prolonged wear and enable a grazing diet. Similarly, low crowned

teeth and other craniodental features can indicate a browsing diet (Solounias and Moelleken, 1993; MacFadden and Shockey, 1997; Mendoza et al., 2002). While tooth morphology can provide insight into the diets of extinct taxa, stable isotope techniques can improve dietary interpretations and identify the presence of relatively dense forest environments (Cerling et al., 1997, 2004; van der Merwe and Medina, 1989, 1991).

Stable carbon isotopes, such as ^{13}C and ^{12}C , naturally occur in plants and vary depending on how a plant photosynthesizes. Taking into account the ^{13}C enrichment from food to tooth enamel ($\sim 14\text{‰}$) as well as the decline in $\delta^{13}\text{C}$ values ($\sim 1.5\text{‰}$) of atmospheric CO_2 due to fossil fuel burning over the past two centuries, tooth enamel values of less than -8‰ indicate a diet consisting of primarily C_3 vegetation whereas $\delta^{13}\text{C}$ values of greater than -2‰ indicate a diet of predominantly C_4 vegetation (Cerling et al., 1997; Cerling and Harris, 1999). Additionally, stable carbon isotope data of extinct taxa can be used to identify ancient forests due to greater ^{13}C discrimination occurring in dense closed canopies as compared to more open C_3 environments (van der Merwe and Medina, 1989; Cerling et al., 2004). Because $\delta^{13}\text{C}$ values increase with decreasing canopy density and/or increasing distance from dense forest edges (van der Merwe and Medina, 1989; Kapos et al., 1993; West et al., 2001), more negative $\delta^{13}\text{C}$ enamel values of mammalian herbivores reflect the consumption of browse in forests with denser canopies (van der Merwe and Medina, 1989, 1991; Cerling et al., 2004). Therefore, $\delta^{13}\text{C}$ values of mammalian tooth enamel can indicate meaningful differences in habitat type within C_3 floral environments and therefore assist in determining relative canopy density in ancient forests.

Through the synergistic combination of ecological “ground-truthing” and paleoecological investigations of late Cenozoic fossil sites, my dissertation consists of a series of research

projects that collectively help to reconstruct ancient forest environments. Specifically, I ask the following key questions:

- How do stable carbon and oxygen isotope analyses of extant tapirs help constrain paleoecological hypotheses? (Chapter 2)
- What was the environment and climate like in the Appalachians during the Neogene? (Chapter 3)
- How are resources partitioned between forest dwelling taxa? (Chapter 3)
- How have forest distributions changed over time in the New World? (Chapter 4)

Using stable isotopes and vertebrate morphology, the answers to these questions provide insight regarding the paleoecology of forest environments and their mammalian inhabitants. This work improves our knowledge of fossil localities and provides the necessary ecological background to further interpret ancient forest environments.

Tapirs are of particular interest because they are potential model organisms for identifying forest environments as they are highly conservative in diet, habitat preference, and migratory behavior (Bodmer, 1990a; Salas, 1996; Henry et al., 2000; Downer, 2001; Tobler, 2002; Foerster and Vaughan, 2002). With a focus on forest-dwelling tapirs and their ancestors, it is necessary to first understand how extant tapirs track carbon and oxygen isotope variation, and the extent of variation at the individual, population, and species level. The second chapter clarifies stable carbon and oxygen isotope variation and provides insight into extant tapir ecology. Additionally, the work discussed in Chapter 2 helps constrain paleoecological interpretations of the fossil sites discussed. The Gray Fossil Site, the most fossiliferous tapir locality in the world, provides rare insight into Neogene paleoecology in the Appalachians region. The Gray Fossil Site was thought to have served as a forest refuge (Wallace and Wang, 2004) during a time of dramatic environmental change, including the expansion of C₄ grasslands globally (Cerling et al., 1997). In Chapter 3, the paleoecology and paleoclimatology of the Gray Fossil Site is inferred based on

the geochemistry of fossil tooth enamel (stable isotopes and Rare Earth Elements). Furthermore, I test the hypothesis that the Gray Fossil Site represents a forested Appalachian refuge during the Neogene. Collectively, these chapters provide the ground work for testing the hypothesis that fossil tapirs are indicators of forest environments. In order to test this idea, I evaluated how craniodental morphology and carbon isotopes of extinct tapirs changed over time, in Chapter 4. Using tapirs as indicators of forests, I then document how forest distributions have changed in the New World throughout the last 55 million years. This body of work will significantly add to the field of paleoecology by improving interpretations of late Cenozoic fossil sites through the integration of ecological and paleoecological research.

The aim of this dissertation is to advance the field of paleoecology and communicate some of the scientific research discussed to the public. Communicating the broader impacts of scientific research to society is a necessary responsibility of scientific researchers. In Appendix A, I discuss the importance of communicating science to the public. In Appendix B, I aim to improve a student's understanding of ancient ecosystems by developing an educational module that allows middle school level students to use actual data to test scientific hypotheses. The goal of the appended unit is to actively engage students in understanding how scientific interpretations and subsequent illustrations are developed. Through inquiry-based activities that allow students to analyze actual scientific data produced in this dissertation, students develop and test hypotheses, later communicating the products of their scientific investigation.

Through the integration of modern ecology, vertebrate paleontology, and scientific outreach, I aim to improve understandings of ancient forest environments and engage the public in the joy of scientific discovery.

CHAPTER 2
STABLE ISOTOPE ECOLOGY OF EXTANT TAPIRS (*TAPIRUS BAIRDII*, *T. PINCHAQUE*,
T. TERRESTRIS) FROM THE AMERICAS

Introduction

The extant tapirs, Baird's tapir (*Tapirus bairdii*), lowland tapir (*Tapirus terrestris*), mountain tapir (*Tapirus pinchaque*), and Malayan tapir (*Tapirus indicus*) occupy forest environments in southern Mexico, Central America, South America and southeast Asia (Salas, 1996; Brooks et al., 1997; Foerster and Vaughan, 2002; Tobler, 2002; Holden et al., 2003). These habitats include lowland forests, primary and secondary forests, Amazonian flood-plains, and montane cloud forests (Terwilliger, 1978; Eisenberg, 1989; Fragoso, 1991; Salas, 1996; Brooks et al., 1997; Downer, 2001; Foerster and Vaughan, 2002; Tobler, 2002; Holden et al., 2003; Lizcano et al., 2004). *T. bairdii* is also found almost exclusively in areas with dense vegetation, and rarely in more open habitats (Tobler, 2002). Even the mountain tapir *T. pinchaque*, which is capable of inhabiting treeless paramo environments of >3800m elevation, lives in dense Andean forests more frequently than any other habitat type (Downer, 2001). Tapirs can also have limited home ranges of approximately 125 ha or less (Foerster and Vaughan, 2002), making them good indicators of their local environments and thus able to provide information about local environments in the fossil record.

Tapirs are browsers with a diet consisting of leaves, twigs, fiber, and fruit (Terwilliger, 1978; Bodmer, 1990a, 1991; Fragoso, 1991; Salas and Fuller, 1996; Henry et al., 2000; Downer, 2001; Galetti et al., 2001; Tobler, 2002; Lizcano and Cavelier, 2004). They primarily browse in forest environments throughout the year (Bodmer, 1990a; Salas, 1996; Tobler, 2002; Foerster and Vaughan, 2002; Henry et al., 2000). Even with seasonal flooding, dietary differences are absent or minor, potentially varying with fruiting events (Bodmer, 1990b; Henry et al., 2000). In addition, their craniodental morphology is highly conservative over time in comparison to

tapiroid fossils (Colbert and Schoch, 1998; DeSantis and MacFadden, 2007) and is similar to that of other extinct and extant browsing mammals (MacFadden and Shockey, 1997; Mendoza et al., 2002). Stable carbon isotope values of tapirs over the past 10 million years similarly indicate that they maintained a diet of predominantly C₃ plants, likely consumed in the denser canopied forests locally available (DeSantis and MacFadden, 2007). However, it is not clear how variable extant tapir diets and subsequent $\delta^{13}\text{C}$ values are at the individual level during ontogeny, at the population and species level, and how environmental and climatic variables influence their $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. In order to better understand the ecology of these elusive mammals both today and in the past, it is critical to understand their stable isotope ecology.

Stable carbon isotopes are incorporated into mammalian tooth enamel, retaining isotopic signatures reflective of ones diet (DeNiro and Epstein, 1978; Krueger, 1991; Lee-Thorp and van der Merwe, 1991; Cerling et al., 1997; Cerling and Harris, 1999). Specifically, $\delta^{13}\text{C}$ signatures of C₃ and C₄ plants are incorporated into the tooth enamel of medium to large bodied herbivorous mammals with an enrichment factor of 14.1‰ (although non-ruminants, including tapirs, may have an enrichment factor between 12 and 13‰; Cerling and Harris, 1999). Based on modern analogues, $\delta^{13}\text{C}$ enamel values < -8‰ reflect a predominantly C₃ diet (e.g. trees, shrubs, and cool season grasses) with more ¹³C depleted values indicating denser canopied environments (MacFadden et al., 1996; Cerling et al., 1997, 1999, 2004; van der Merwe and Medina, 1989, 1991; Cerling and Harris, 1999). Variation in $\delta^{13}\text{C}$ values between individual teeth can also indicate seasonal differences in diet, potentially reflective of seasonal changes in vegetation due to water stress (Roux et al., 2001; Ehleringer et al., 2002). As $\delta^{13}\text{C}$ signatures do not change with time during the process of fossilization, ratios from fossil mammals can be interpreted as similar to those of today, plus ~1.5‰ due to modern atmospheric CO₂ enrichment

(Ehleringer and Monson, 1993; Cerling et al., 1997; Passey et al., 2002). However, in order to properly interpret the $\delta^{13}\text{C}$ values of fossil mammals including tapirs, it is first necessary to understand $\delta^{13}\text{C}$ variation in extant individuals, populations, species, and across varying climatic regimes.

Stable oxygen isotopes are similarly incorporated into mammalian tooth enamel. Instead of a diet signal as with $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ values are a function of body water that reflects the response of meteoric water to changes in temperature and/or precipitation/humidity (Dansgaard, 1964; Longinelli, 1984; Bryant et al., 1994, 1996a,b; Bryant and Froelich, 1995; Bocherens et al., 1996; Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999; Higgins and MacFadden, 2004; MacFadden and Higgins, 2004; Hoppe, 2006). In terrestrial ecosystems, seasonal variation is recorded in tooth enamel with higher $\delta^{18}\text{O}$ values indicating high summer temperatures as compared to lower $\delta^{18}\text{O}$ values during cooler winters (Fricke and O'Neil, 1996; Feranec and MacFadden, 2000; MacFadden and Higgins, 2004). Oxygen isotopes of mammalian tooth enamel can also vary between or among taxa occupying similar environments due to variations in the proportion of drinking water ingested, as opposed to more evaporated plant water (Levin et al., 2006). Mammals that obtain a large proportion of their water from drinking are thought to be insensitive to large changes in $\delta^{18}\text{O}$ values with increased aridity, as opposed to taxa that obtain a larger portion of their water from plants (Levin et al., 2006). Tapirs are thought to track meteoric water based on their consumption of water from free water sources (e.g. rivers and lakes) and prolonged periods of time spent in the water (Bodmer, 1990b). However, extinct tapirs during the Pliocene and Pleistocene show a significant decline in $\delta^{18}\text{O}$ values with increased aridity associated with interglacial warming (DeSantis et al., 2009). Thus, it is critical to understand how $\delta^{18}\text{O}$ enamel values of extant tapirs are associated with climatic variables including

precipitation and temperature. Clarifying these relationships will enable a better understanding of the ecology of extant tapirs and allow for informed interpretations of the paleoecology and paleoclimatology of fossil sites containing fossil tapirs.

Here, $\delta^{13}\text{C}$ variation of extant tapirs from throughout the Americas is assessed to determine how $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values vary over the first few years of a tapir's life, at the population and species level, and how climatic variables including precipitation and temperature affect $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. Individual and population variation is first examined in a Mexican population of Baird's tapir (*Tapirus bairdii*) by first comparing early and late erupting teeth to evaluate the potential effects of weaning on $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. Second, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variation is quantified at the population level to determine dietary resource use and further evaluate if a small number of specimens can reliably estimate a population's mean. Third, species level $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variability is quantified in *T. bairdii*, the lowland tapir (*Tapirus terrestris*) and the mountain tapir (*Tapirus pinchaque*); subsequently, quantifying the effects of climatic (i.e. temperature and precipitation) and geographic (i.e. latitude and elevation) parameters on $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values at the genus and species level. This work enables a better understanding of the ecology of extant tapirs while also constraining paleoecological interpretations of extinct tapirs and their environments through time.

Materials and Methods

Extant tapirs (*T. bairdii*) from Mexico were sampled from the Osteological Collection at the Yale Peabody Museum (YPM) in order to quantify dietary variation and potential ontogenetic dietary shifts, as inferred from stable isotopes. The 11 individuals sampled were initially collected within the two-year period of 1873-1874 in Acapulco, Mexico. Because the osteological specimens of *T. bairdii* were collected from the same general area, $\delta^{13}\text{C}$ variation can be attributed to dietary variation. Ontogenetic diet shifts were quantified by comparing early

erupting first molars (M1) to late erupting fourth premolars (P4) and third molars (M3) of like individuals. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of different tooth positions were compared to one another using paired Student's t-tests as these data were normally distributed (Shapiro-Wilks test). Similar to the work of Clementz and Koch (2001), I conducted a power analysis to test if small sample sizes of tapir teeth are likely to represent a population's mean. By comparing population means with the mean of three randomly selected samples, I assessed if three samples can approximate a population mean (as estimated from the $\delta^{13}\text{C}$ values from one or more tooth positions). Each tooth was assigned a number from 1-33 and a random number generator was used to select three teeth, replicated 100 times per tooth eruption category. The resulting mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of M1s, P4s, M3s, late erupting teeth (P4s and M3s), and all tooth positions were compared to population means, and differences between the sample mean and population mean were calculated.

In addition to the *T. bairdii* specimens from Acapulco, Mexico, extant tapirs (*T. bairdii*, n = 19; *T. terrestris*, n = 15; and *T. pinchaque*, n = 3) were also sampled from Mexico, Central America, and South America based on specimens in the American Museum of Natural History (AMNH) Mammalogy Collection (Figure 2-1, Table 2-1). Late erupting third molars (or fourth premolars when third molars had not erupted) were sampled from these specimens. All specimens selected are associated with geographic information stating where they were collected. Based on the geographic information, data from the closest climate stations were associated with respective $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (National Climatic Data Center, 2009; Table 2-1). Mean data from two climate stations were averaged when specimens were located approximately equidistant from them. Data from as many years as were available were included; however, equal numbers of months was kept consistent (e.g. if only 10 January months were

available, then only 10 February, 10 March, 10 April, etc.. months were included). The climatic data compiled and analyzed include, the following (with abbreviations and units noted): mean monthly temperature (MT, °C), mean monthly precipitation (MP, mm), precipitation frequency (PF, mean number of precipitation days per month), and estimated $\delta^{18}\text{O}$ local precipitation values ($\delta^{18}\text{O}_p$, computed using the Online Isotopes in Precipitation Calculator available at www.waterisotopes.org, based on latitude, longitude, and elevation). Geographic information, including latitude (absolute value of decimal degrees north) and elevation (m) were also included in the analysis. Mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were compared at the species level using both parametric ANOVA Fisher LSD and non-parametric Kruskal-Wallis tests. I assessed which climatic, geographic, and isotopic variables were correlated (Pearson correlations) with $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values. Multiple regressions were used to assess the contribution of the climatic and geographic variables to $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. Variables that were highly correlated, Pearson correlation coefficients ≥ 0.95 were removed from individual analyses. Linear regressions were used to determine the relationship between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ enamel values from like specimens. Additionally, linear regressions were used to determine the relationship between $\delta^{18}\text{O}$ enamel values and estimated $\delta^{18}\text{O}$ local precipitation values. All analyses were done at the generic level (including all *Tapirus* species except *Tapirus indicus*, due to its geographic distance from the remainder of the taxa) and species level (with the added exception of *Tapirus pinchaque* due to limited sample size, $n = 3$).

All enamel samples were acquired by drilling approximately 2-3 mg of sample using a low speed Foredom™ drill and carbide dental burrs. All enamel powder was pretreated with 30% hydrogen peroxide for 24 hours and 0.1N acetic acid for 12 hours to remove organics and secondary carbonates, respectively (Koch et al., 1997). These samples (~1 mg) were run on a

VG Prism stable isotope ratio mass spectrometer with an in-line ISOCARB automatic sampler in the Department of Geological Sciences at the University of Florida. The analytical precision is +/- 0.1‰. Normalized data (to NBS-19) are reported in conventional delta (δ) notation for carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$), where $\delta^{13}\text{C}$ (parts per mil, ‰) = $((R_{\text{sample}}/R_{\text{standard}})-1) * 1000$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$; and, $\delta^{18}\text{O}$ (parts per mil, ‰) = $((R_{\text{sample}}/R_{\text{standard}})-1) * 1000$, and $R = {}^{18}\text{O}/{}^{16}\text{O}$; and the enamel carbonate standard is VPDB (Pee Dee Belemnite, Vienna Convention; Coplen, 1994).

Results

Individual and Population Level Variation (*T. bairdii*)

$\delta^{13}\text{C}$ values of late erupting (P4 and M3) teeth are significantly greater (by 1.5‰ to 1.7‰) than the early erupting first molar ($p < 0.0001$ for both paired Student's t-tests of M1-P4, and M1-M3; Table 2-2 and 2-3). The $\delta^{18}\text{O}$ values do not show this same pattern, with M1 and P4 teeth sharing identical means (-5.8‰). Instead $\delta^{18}\text{O}$ values of P4 and M3 teeth are significantly different from each other (difference of -0.5‰, $p = 0.004$). Additionally, dietary variation at the population level is low with total $\delta^{13}\text{C}$ variation of 2.2‰, 2.3‰, and 2.9‰ for M1s, P4s, and M3s, respectively (Figure 2-2). Similarly, $\delta^{18}\text{O}$ variation is low with total variation of 2.6‰, 1.4‰, and 2.2‰ for M1s, P4s, and M3s, respectively (Figure 2-2).

Based on comparisons of the stable isotope values of three randomly selected samples to population means, only a few samples are required to approximate population means. This is because the mean $\delta^{13}\text{C}$ values of randomly selected sub-samples were consistently within 1.5‰ of the population mean, with average variation of 0.3‰ for P4, 0.4‰ for M3, 0.4‰ for late erupting teeth (P4s and M3s), and 0.5‰ for all sampled teeth (M1s, P4s, and M3s). Mean $\delta^{18}\text{O}$ values were also all within 1.1‰ (with an average difference of 0.3‰) using all combinations of tooth positions sampled.

Species Level Variation (*T. bairdii*, *T. pinchaque*, *T. terrestris*)

Mean $\delta^{13}\text{C}$ values (\pm 1 SD) of *T. bairdii*, *T. pinchaque*, and *T. terrestris* are $-14.8 \pm 0.9\text{‰}$, $-14.3 \pm 1.4\text{‰}$, and $-15.6 \pm 1.6\text{‰}$, respectively (Figure 2-3). The $\delta^{13}\text{C}$ values of *T. terrestris* range from -18.1‰ to -12.8‰ , yielding the greatest total range (5.3‰) as compared to *T. bairdii* (ranging from -16.4‰ to -13.0‰ , total range of 3.4‰) and *T. pinchaque* (ranging from -15.9 to -13.1‰ , total range of 2.8‰ ; Figure 2-3). *T. terrestris* also has individuals with the lowest $\delta^{13}\text{C}$ values of all species sampled. However, $\delta^{13}\text{C}$ values of *T. bairdii*, *T. pinchaque*, and *T. terrestris* are not significantly different from one another. Mean $\delta^{18}\text{O}$ values (\pm 1 SD) of *T. bairdii*, *T. pinchaque*, and *T. terrestris* are $-4.5 \pm 1.5\text{‰}$, $-8.0 \pm 0.4\text{‰}$, and $-3.3 \pm 1.4\text{‰}$, ranging from -6.0‰ to -0.4‰ , -8.4‰ to -7.6‰ , and -5.2‰ to -0.9‰ , respectively (Figure 2-3). In contrast, the $\delta^{18}\text{O}$ values of these tapirs are significantly different from one another ($p = 0.001$; Kruskal-Wallis), with $\delta^{18}\text{O}$ values of *T. pinchaque* significantly less than both *T. bairdii* ($p < 0.001$; Fisher LSD) and *T. terrestris* ($p < 0.0001$; Fisher LSD). The $\delta^{18}\text{O}$ values of *T. bairdii* are also significantly less than *T. terrestris* ($p = 0.021$; Fisher LSD).

Climatic and Geographic Parameters (*T. bairdii*, *T. pinchaque*, *T. terrestris*)

The $\delta^{18}\text{O}$ values of all extant tapirs analyzed (*T. bairdii*, *T. pinchaque*, *T. terrestris*) are negatively correlated with elevation (-0.48 , $p = 0.003$; Table 2-4). Multiple linear regressions demonstrate that precipitation frequency (the mean number of precipitation days per month) has the greatest relative weight (standardized coefficients \pm standard error, and p -values noted; 2.04 ± 0.29 , $p < 0.0001$), followed by mean total precipitation (-1.35 ± 0.23 , $p < 0.001$), elevation (-1.03 ± 0.20 , $p < 0.0001$), latitude (0.80 ± 0.17 , $p < 0.0001$), and estimated $\delta^{18}\text{O}$ local precipitation values (-0.50 ± 0.20 , $p = 0.016$). The multiple linear regression model, $\delta^{18}\text{O}$ enamel values = $-12.6 - 0.87 \cdot \text{PF} - 3.45 \cdot \text{MP} + 0.26 \cdot \text{latitude} - 0.78 \cdot \delta^{18}\text{O}_p - 0.004 \cdot \text{elevation}$, explains $\sim 75\%$ of the variation in tapir $\delta^{18}\text{O}$ enamel values ($R^2 = 0.75$, adjusted $R^2 = 0.71$, $p <$

0.0001). Mean monthly temperatures were removed from the analysis as they are highly correlated with elevations ($-0.95, p < 0.0001$) and elevation is more correlated with $\delta^{18}\text{O}$ values ($-0.48, p = 0.003$) than mean monthly temperature ($0.38, p = 0.019$; Table 2-4). The $\delta^{13}\text{C}$ values of all tapirs are instead negatively correlated with mean total monthly precipitation ($-0.50, p = 0.002$; Table 2-4). A multiple linear regression model was similarly developed to assess the weight of the contributions of climatic and geographic variables on $\delta^{13}\text{C}$ values, with the additional exclusion of the estimated average $\delta^{18}\text{O}$ precipitation variable. None of the variables analyzed are significant, and the model only accounts for $\sim 30\%$ of the variation ($R^2 = 0.30, p = 0.021$).

Stable carbon and oxygen isotope values of *T. bairdii* and *T. terrestris* were analyzed at the species level to determine which variables were correlated with $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variation. The $\delta^{18}\text{O}$ enamel values are positively correlated with both precipitation variables, precipitation frequency ($0.84, p < 0.0001$) and mean monthly precipitation ($0.63, p = 0.004$), and negatively correlated with estimated $\delta^{18}\text{O}$ local precipitation values ($-0.76, p = 0.0002$) in *T. bairdii* (Table 2-4). Mean number of precipitation days explains $\sim 70\%$ ($R^2 = 0.70, p < 0.0001, y = 0.56x - 7.8$) of the variation in *T. bairdii* $\delta^{18}\text{O}$ enamel values (Figure 2-4). Additionally, estimated $\delta^{18}\text{O}$ local precipitation values explain $\sim 58\%$ ($R^2 = 0.58, p = 0.0002, y = -2.14x - 13.41$) of the variation in *T. bairdii* $\delta^{18}\text{O}$ enamel values. A multiple linear regression model incorporates precipitation frequency, mean monthly temperatures, and estimated $\delta^{18}\text{O}$ local precipitation values, as all other variables were removed due to multicollinearity. *T. bairdii* $\delta^{18}\text{O}$ enamel values = $-68.1 + 1.14*\delta^{18}\text{O}_p + 2.24*MT + 1.14*PF$ ($R^2 = 0.80, \text{adjusted } R^2 = 0.76, p < 0.0001$), with precipitation frequency yielding the greatest standardized coefficient (\pm stand error) of 1.72 ± 0.48 ($p = 0.003$) followed by mean monthly temperature with a value of 0.72 ± 0.30 ($p = 0.026$). The

$\delta^{13}\text{C}$ enamel values of *T. bairdii* are not correlated with any climatic or geographic variable, nor are they correlated with $\delta^{18}\text{O}$ enamel values of like specimens (Table 2-4).

T. terrestris $\delta^{18}\text{O}$ enamel values are positively correlated with latitude (0.68, $p = 0.005$) and negatively correlated with mean monthly precipitation (-0.61, $p = 0.016$; Table 2-4). *T. terrestris* $\delta^{18}\text{O}$ enamel values = $81.5 - 1.04*\delta^{18}\text{O}_p - 3.17*MT + 0.65*PF - 5.62*MP - 1.36*\text{latitude} - 2.68*\text{elevation}$ ($R^2 = 0.89$, adjusted $R^2 = 0.80$, $p = 0.002$), with mean monthly precipitation yielding the greatest standardized coefficient (+/- stand error) of -3.12 +/- 0.84 ($p = 0.006$) followed by precipitation frequency with a value of -1.66 +/- 0.59 ($p = 0.023$). *T. terrestris* $\delta^{18}\text{O}$ enamel values are not significantly correlated with estimated local precipitation $\delta^{18}\text{O}$ values (Table 2-4). Similarly, $\delta^{13}\text{C}$ enamel values of *T. terrestris* are negatively correlated with mean monthly precipitation (-0.56, $p = 0.031$) and positively correlated with latitude (0.78, $p = 0.001$; Table 2-4) and with $\delta^{18}\text{O}$ enamel values of like specimens (0.93, $p < 0.0001$). Although ~83% of the variation in *T. terrestris* $\delta^{13}\text{C}$ enamel values is explained using the following regression: $\delta^{13}\text{C}$ enamel values = $17.41 - 1.3*MT - 0.02*MP + 0.28*\text{latitude} - 0.014*\text{elevation} + 0.37*PF$ ($R^2 = 0.83$, adjusted $R^2 = 0.73$, $p = 0.003$), none of the included variables significantly contribute. However, $\delta^{13}\text{C}$ enamel values explain ~85% ($R^2 = 0.86$, adjusted $R^2 = 0.85$, $p < 0.001$, $y = 9.95 + 0.85x$) of the variation in $\delta^{18}\text{O}$ enamel values in *T. terrestris* (Figure 2-5).

Discussion

Implications of Ontogenetic and Population Level Variation

Previous work has documented ^{18}O enrichment in early erupting teeth due to weaning from the mother's milk at the time of mineralization (Bryant and Froelich, 1995; Bryant et al., 1996a,b; Fricke and O'Neil, 1996; Zazzo et al., 2002). Although tapirs are expected to exhibit the same pattern, $\delta^{18}\text{O}$ values of early and late erupting teeth are not significantly different.

Instead, $\delta^{18}\text{O}$ values of the late erupting P4 and M3 teeth are significantly different, likely due to differences in seasonality. As the M3 erupts after the P4 (based on the examination of tapir specimens at the AMNH and YPM), these teeth are likely reflecting the $\delta^{18}\text{O}$ values of subsequent seasons that vary due to either temperature and/or precipitation. Additionally, because temperature is not highly variable (i.e. ~ 3 °C variation between the lowest and highest monthly mean temperatures; National Climatic Data Center, 2009) in Acapulco, Mexico whereas the region does exhibit a distinct wet and dry season (i.e. on average 6 months out of the year experience < 2 days of precipitation per month; National Climatic Data Center, 2009), seasonal precipitation differences are the most likely explanation for the significant differences between late erupting teeth. However, $\delta^{18}\text{O}$ values of early erupting teeth may still be recording a weaning signal that is swamped out by differences in precipitation regimes.

In contrast, $\delta^{13}\text{C}$ values of early erupting M1 teeth are significantly different from both of the late erupting teeth (P4 and M3), suggesting ontogenetic dietary differences. These differences may be due to the consumption of lipid-rich milk that is ^{13}C depleted (DeNiro and Epstein, 1978; Tieszen et al., 1983; Hobson and Sease, 1998) or due to the consumption of browse in a denser canopy than occupied during adulthood (van der Merwe and Medina, 1989, 1991; Cerling et al., 2004). As the striped and spotted pelage of juvenile tapirs is thought to help with concealment from predators (e.g. the puma; Eisenberg, 1989), their presence in a denser canopy during juvenile years may further help protect them against predation. Alternatively, juvenile tapirs may be consuming a larger proportion of ^{13}C depleted leaves and subsequently consuming a lower proportion of ^{13}C enriched fruits (Cerling et al., 2004; Codron et al., 2005). Although it is difficult to discern the exact reason for ^{13}C depletion in early

erupting teeth, assessment of dietary variation at the population or species level should include like tooth positions to avoid ontogenetic dietary differences.

Low $\delta^{13}\text{C}$ variation of *T. bairdii* at the population level is consistent with their inferred conservative diet. Although $\delta^{13}\text{C}$ variation only captures an aspect of dietary variation, limited $\delta^{13}\text{C}$ variation indicates the consumption of food items with similar $\delta^{13}\text{C}$ values and/or from forests with similar canopy density. Low $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variation at the population level makes tapirs ideal taxa for discerning environmental and climatic variation. Further sub-sampling also established that $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ mean values of three randomly selected teeth, from both similar and different tooth positions, estimates the population mean. This is critical for inferring past environments as often tapir fossils are a rare component of a fauna, and the specimens available may be from teeth that erupted at different times. Thus, the stable isotope analysis of three or more extinct or extant tapir teeth is likely to estimate a population's mean. Therefore, stable carbon isotope analyses of extinct tapirs can help elucidate past diets and forest structure, while modern tapir isotopic data can be compared to museum specimens to understand dietary variation over time.

Influence of Climatic and Geographic Variables

All tapirs (*T. bairdii*, *T. pinchaque*, *T. terrestris*) have $\delta^{13}\text{C}$ values consistent with a predominantly C_3 diet, with all values less than -12‰ . *T. terrestris* also has individuals with the lowest $\delta^{13}\text{C}$ values of all species sampled ($<16.5\text{‰}$), suggesting their consumption of browse in the densest canopied environments. This interpretation is consistent with their presence in dense Amazonian rainforests. Alternatively, lower $\delta^{13}\text{C}$ values may be indicative of a diet consisting of fewer ^{13}C enriched fruits (Cerling et al., 2004; Codron et al., 2005). Furthermore, all $\delta^{13}\text{C}$ values of *T. pinchaque* teeth are consistent with their consumption of browse in forest

environments, further supporting their utilization of forest environments despite their ability to exist in treeless paramo environments (Downer, 2001).

Significantly different $\delta^{18}\text{O}$ values between all tapirs likely reflects climatic differences influencing local meteoric water consumed and potential differences in tapir behavior. The $\delta^{18}\text{O}$ values of *T. pinchaque* are the lowest due to their presence in high elevation environments. With increased elevation, the heavier ^{18}O isotope is preferentially rained out leaving ^{18}O depleted rainfall at higher elevations (Poage and Chamberlain, 2001). Any water consumed via free water sources or plant water has lighter $\delta^{18}\text{O}$ values than water at lower elevations. The significant contributions of elevation and estimated $\delta^{18}\text{O}$ values of local precipitation towards explaining $\delta^{18}\text{O}$ values are consistent with the pattern of lower $\delta^{18}\text{O}$ values with increasing elevation. Once tapirs are analyzed at the species level and the high elevation *T. pinchaque* is excluded from analyses, elevation is less of a contributing factor to either *T. bairdii* $\delta^{18}\text{O}$ values or *T. terrestris* $\delta^{18}\text{O}$ values. Although *T. bairdii* $\delta^{18}\text{O}$ values are positively correlated with elevation, this pattern is in contrast to biogeochemical processes (i.e. decreased precipitation $\delta^{18}\text{O}$ values with increased elevation, Poage and Chamberlain, 2001) and is unlikely a driving factor as all *T. bairdii* specimens are from elevations of < 60 m. Instead, precipitation variables are greater contributors to *T. bairdii* and *T. terrestris* $\delta^{18}\text{O}$ values than elevation.

T. terrestris has the greatest $\delta^{18}\text{O}$ values, significantly greater than both *T. bairdii* and *T. pinchaque*. These differences in $\delta^{18}\text{O}$ values are likely due to climatic variables. Mammals living in more arid and/or warmer areas are predicted to have either similar or greater $\delta^{18}\text{O}$ values with decreased precipitation (Levin et al., 2006); however, this pattern is in contrast to what is observed here. Instead, *T. bairdii* $\delta^{18}\text{O}$ values increase with increased precipitation (both frequency and amount; Figure 2-4). This pattern may instead demonstrate that *T. bairdii* is

changing its behavior when present in dryer areas, drinking a greater proportion of ^{18}O deplete water from lakes and rivers when precipitation is low. These differences in precipitation may further be amplified by severe dry seasons that are more typical in *T. bairdii* regions such as Acapulco, Mexico (yielding < 2 days of precipitation per month for six months per year; National Climatic Data Center, 2009). Temperature may further influence *T. bairdii* drinking behavior, as higher temperatures are here correlated with lower $\delta^{18}\text{O}$ values, and thus indicative of increased drinking. This is in contrast to the typical pattern of increased $\delta^{18}\text{O}$ values with increased temperature (Fricke and O'Neil, 1996; Feranec and MacFadden, 2000; MacFadden and Higgins, 2004), further supporting the hypothesis that tapirs are changing their drinking behavior. *T. terrestris* $\delta^{18}\text{O}$ values are instead negatively correlated with mean monthly precipitation, demonstrating that tapirs present in areas with higher precipitation (e.g. water is no longer a limiting factor) may instead respond as predicted.

The $\delta^{13}\text{C}$ values of *T. terrestris* explain the majority of the variation in $\delta^{18}\text{O}$ values. As evaporation is low in denser canopied forests (Klaassen, 2001), lower $\delta^{18}\text{O}$ values in plant tissues are expected to occur in denser forests with lower $\delta^{13}\text{C}$ values. Therefore, the observed correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values is expected if *T. terrestris* is obtaining a large proportion of its water from plant leaves in the forest understory. As *T. terrestris* is present in wetter Amazonian rainforests, it is likely that *T. terrestris* is consuming a greater proportion of its water from plant leaves as compared to *T. bairdii* which may need to supplement its water intake by drinking more from free water sources (e.g. lakes and rivers). This is further evidenced by *T. bairdii* individuals present in areas with a higher precipitation frequency (≥ 5 days per month), which demonstrates a similar correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (Figure 2-5). Additionally, variation in *T. bairdii* $\delta^{18}\text{O}$ values are largely explained by estimated $\delta^{18}\text{O}$ local

precipitation values. This pattern is expected if *T. bairdii* is obtaining a large portion of water from free water sources. Although tapirs do not occur far from permanent water sources (Eisenberg, 1989), the proportion of water they consume via drinking may change with climatic parameters. Thus, tapirs may present a different relationship from the evaporation sensitive (i.e. $\delta^{18}\text{O}$ values increase with increased aridity) and evaporation insensitive (i.e. $\delta^{18}\text{O}$ values are relatively unchanged with increased aridity) taxa mentioned by Levin et al. (2006). Instead, tapirs exhibit decreased $\delta^{18}\text{O}$ values with increased aridity. This is due to the need to adapt and change behavior, i.e. drink more ^{18}O depleted water, when present in dryer areas (defined according to precipitation frequency and/or amount). Thus, the previously mentioned example demonstrating a significant decline in tapir $\delta^{18}\text{O}$ values with interglacial warming in Florida (DeSantis et al., 2009) suggests increased aridification based on tapir $\delta^{18}\text{O}$ values. Furthermore, the strength of the relationship between *T. terrestris* $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values indicates that tapirs may consume a large proportion of their body water from plant leaves when precipitation is not a limiting factor. A tapir that gets a significant portion of its water from leaves may consume less water from rivers and open water. While it is unclear how adaptable an individual tapir is to changing its behavior in response to its local environment, further study of extant tapir species (e.g. *T. terrestris* vs. *T. bairdii*) may elucidate their adaptability and differences in the relative proportion of time spent in or consuming water from rivers and lakes.

Conclusions

In summary, low population variation in carbon and oxygen isotopes makes tapirs ideal taxa for inferring paleoenvironments, even when only low sample sizes are available, as is characteristically the case in many fossil assemblages. Tapir stable oxygen isotopes vary between species and are largely influenced by precipitation (both amount and frequency). Oxygen isotope variation at the species level is largely a function of precipitation and $\delta^{13}\text{C}$

values in *T. bairdii* and *T. terrestris*, respectively. This is in contrast to the expectation that tapir $\delta^{18}\text{O}$ values will most accurately reflect $\delta^{18}\text{O}$ meteoric water values. While $\delta^{18}\text{O}$ values of *T. bairdii* do show a strong relationship with estimated $\delta^{18}\text{O}$ precipitation values, these values are further influenced by climatic and geographic variables. Additionally, tapirs appear to change their drinking behavior (i.e. relative proportion of free water consumed) with precipitation. This demonstrates the adaptability of tapirs to compensate for low water availability, by increasing drinking behavior. A detailed understanding of modern tapir ecology also helps elucidate paleoecological and paleoclimatic interpretations.

Table 2-1. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of extant tapirs (*Tapirus bairdii*, *Tapirus pinchaque*, and *Tapirus terrestris*) noting climate stations and associated climatic and geographic variables.

Taxon	Museum	ID	TP	$\delta^{13}\text{C}_e$	$\delta^{18}\text{O}_e$	Country	Climate Station	MT	PF	MP	L	E	$\delta^{18}\text{O}_p$
<i>Tapirus bairdii</i>	AMNH	29455	lm3	-16.4	-3.6	Nicaragua	78741	27.3	8.1	108.7	12.15	56	-5.1
<i>Tapirus bairdii</i>	AMNH	29526	lm3	-14.5	-3.3	Nicaragua	78741	27.3	8.1	108.7	12.15	56	-5.1
<i>Tapirus bairdii</i>	AMNH	35000	lm3	-15.4	-3.5	Nicaragua	78741	27.3	8.1	108.7	12.15	56	-5.1
<i>Tapirus bairdii</i>	AMNH	80075	lm3	-15.0	-1.9	Honduras	78705	26.6	11.3	206.6	15.73	26	-4.9
<i>Tapirus bairdii</i>	AMNH	80076	lp4	-14.2	-0.4	Honduras	78705	26.6	11.3	206.6	15.73	26	-4.9
<i>Tapirus bairdii</i>	AMNH	204706	LM3	-14.3	-3.5	Mexico	76833	28.4	3.9	71.3	16.17	2	-4.1
<i>Tapirus bairdii</i>	AMNH	206834	lm3	-14.7	-4.6	Mexico	76833	28.4	3.9	71.3	16.17	2	-4.1
<i>Tapirus bairdii</i>	AMNH	208259	lm3	-15.9	-5.9	Mexico	76833	28.4	3.9	71.3	16.17	2	-4.1
<i>Tapirus bairdii</i>	YPM	6712	RM3	-13.3	-4.9	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	7132	RM3	-15.6	-5.6	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	7133	RM3	-14.3	-5.8	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	7135	RM3	-15.9	-5.2	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	7136	RM3	-14.3	-5.8	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	7140	RM3	-14.3	-5.5	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	7141	RM3	-15.3	-5.3	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	7143	RM3	-14.0	-4.6	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	7477	RM3	-14.9	-6.0	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	8626	RM3	-15.7	-3.8	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus bairdii</i>	YPM	9398	RM3	-13.0	-5.9	Mexico	76805	27.4	5	115.9	16.08	3	-3.8
<i>Tapirus pinchaque</i>	AMNH	70521	lp4	-15.9	-8.4	Ecuador	84179	20.8	20.3	341.1	-1.5	960	-6.9
<i>Tapirus pinchaque</i>	AMNH	149331	lm3	-13.1	-7.6	Colombia	80342	19.3	9.7	90	1.42	1826	-8.5
<i>Tapirus pinchaque</i>	AMNH	149332	lp4	-13.9	-8.0	Colombia	80342	19.3	9.7	90	1.42	1826	-8.5
<i>Tapirus terrestris</i>	AMNH	14690	lm3	-15.7	-3.2	Colombia	80009	28.3	4.2	43.2	11.13	14	-4.6
<i>Tapirus terrestris</i>	AMNH	36661	lm3	-14.0	-2.4	Brazil	83361	26.1	9	125.2	-15.55	151	-5
<i>Tapirus terrestris</i>	AMNH	36662	lm3	-12.8	-0.9	Brazil	83361	26.1	9	125.2	-15.55	151	-5
<i>Tapirus terrestris</i>	AMNH	36663	lm3	-13.0	-1.2	Brazil	83361	26.1	9	125.2	-15.55	151	-5
<i>Tapirus terrestris</i>	AMNH	73596	lm3	-16.4	-4.9	Peru	84377	25.6	14.7	304.4	-3.78	126	-5.2
<i>Tapirus terrestris</i>	AMNH	73766	lm3	-17.0	-5.2	Peru	84377	25.6	14.7	304.4	-3.78	126	-5.2
<i>Tapirus terrestris</i>	AMNH	77573	lm3	-16.8	-4.7	Venezuela	80457	26.8	12.6	188	5.6	74	-4
<i>Tapirus terrestris</i>	AMNH	77576	lm3	-16.3	-3.8	Venezuela	80457	26.8	12.6	188	5.6	74	-4
<i>Tapirus terrestris</i>	AMNH	78518	lm3	-16.6	-4.0	Venezuela	80457	26.8	12.6	188	5.6	74	-4
<i>Tapirus terrestris</i>	AMNH	95133	lm3	-15.3	-2.6	Brazil	82331	27	12.7	187	-3.13	72	-5
<i>Tapirus terrestris</i>	AMNH	96130	lm3	-15.4	-2.3	Brazil	82191	26.6	18.9	261.6	-1.45	10	-2.8

Table 2-1 Continued.

Taxon	Museum	ID	TP	$\delta^{13}\text{C}_e$	$\delta^{18}\text{O}_e$	Country	Climate Station	MT	PF	MP	L	E	$\delta^{18}\text{O}_p$
<i>Tapirus terrestris</i>	AMNH	120996	lm3	-13.5	-1.4	Brazil	83611	23	8.6	122	-20.45	530	-5.5
<i>Tapirus terrestris</i>	AMNH	142280	lp4	-18.1	-5.1	Colombia	80315, 80234	24.8	13.8	191.8	-10.95	270	-5.6
<i>Tapirus terrestris</i>	AMNH	209139	LM3	-16.3	-4.3	Bolivia	85043	26.9	8.3	141.4	-11	141	-5.7
<i>Tapirus terrestris</i>	AMNH	217150	lm3	-16.6	-3.1	Bolivia	85245, 85154	25.9	11.0	166.6	-10.98	206	-5.4

Note: Table abbreviations and scales are defined as follows: Taxon, taxonomic name; Museum, museum location of sampled specimen; ID, specimen identification number; TP, tooth positions with capital text indicating upper teeth, listing the side (left or right), tooth (premolar or molar), and exact position (number); $\delta^{13}\text{C}_e$, $\delta^{13}\text{C}$ enamel values (VPDB, ‰); $\delta^{18}\text{O}_e$, $\delta^{18}\text{O}$ enamel values (VPDB, ‰); Country, country of origination; Climate Station, location where all climate data were compiled and estimates of local $\delta^{18}\text{O}$ precipitation values were estimated; MT, mean monthly temperature (°C); PF, precipitation frequency (mean number of precipitation days per month); MP, mean monthly precipitation (mm); L, latitude (decimal degrees north); E, elevation (m); $\delta^{18}\text{O}_p$, estimated $\delta^{18}\text{O}$ values of local precipitation calculated using the Online Isotopes in Precipitation Calculator available at www.waterisotopes.org, based on latitude, longitude, and elevation (VSMOW, Vienna Standard Mean Ocean Water, ‰).

Table 2-2. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from a population of extant tapirs (*Tapirus bairdii*) in Acapulco, Mexico.

YPM ID	$\delta^{13}\text{C}_{(\text{VPDB}, \text{‰})}$			$\delta^{18}\text{O}_{(\text{VPDB}, \text{‰})}$		
	M1	P4	M3	M1	P4	M3
6712	-16.1	-14.3	-13.3	-5.3	-5.5	-4.9
7132	-16.4	-15.3	-15.6	-5.7	-6.2	-5.6
7133	-15.9	-14.9	-14.3	-5.5	-6.5	-5.8
7135	-16.0	-15.4	-15.9	-5.5	-5.2	-5.2
7136	-15.3	-14.5	-14.3	-5.9	-6.5	-5.8
7140	-16.0	-14.7	-14.3	-6.3	-5.9	-5.5
7141	-17.5	-14.6	-15.3	-4.8	-5.2	-5.3
7143	-15.8	-14.6	-14.0	-5.4	-5.4	-4.6
7477	-17.4	-15.5	-14.9	-7.4	-6.4	-6.0
8626	-17.1	-15.7	-15.7	-5.6	-5.1	-3.8
9398	-16.1	-13.4	-13.0	-6.3	-5.8	-5.9
mean	-16.3	-14.8	-14.6	-5.8	-5.8	-5.3
SD	0.7	0.4	0.9	0.7	0.5	0.7
min	-17.5	-15.7	-15.9	-7.4	-6.5	-6.0
max	-15.3	-13.4	-13.0	-4.8	-5.1	-3.8
range	2.2	2.3	2.9	2.6	1.4	2.2

Table 2-3. Stable carbon and oxygen isotope differences between various early and late erupting tooth positions, from a population of extant tapirs (*Tapirus bairdii*) in Acapulco, Mexico.

YPM ID	$\delta^{13}\text{C}_{(\text{VPDB}, \text{‰})}$ Differences			$\delta^{18}\text{O}_{(\text{VPDB}, \text{‰})}$ Differences		
	M1-P4	M1-M3	P4-M3	M1-P4	M1-M3	P4-M3
6712	-1.8	-2.8	-1	0.2	-0.4	-0.6
7132	-1.1	-0.8	0.3	0.5	-0.1	-0.6
7133	-1	-1.6	-0.6	1	0.3	-0.7
7135	-0.6	-0.1	0.5	-0.3	-0.3	0
7136	-0.8	-1	-0.2	0.6	-0.1	-0.7
7140	-1.3	-1.7	-0.4	-0.4	-0.8	-0.4
7141	-2.9	-2.2	0.7	0.4	0.5	0.1
7143	-1.2	-1.8	-0.6	0	-0.8	-0.8
7477	-1.9	-2.5	-0.6	-1	-1.4	-0.4
8626	-1.4	-1.4	0	-0.5	-1.8	-1.3
9398	-2.7	-3.1	-0.4	-0.5	-0.4	0.1
mean	-1.5	-1.7	-0.2	0.0	-0.5	-0.5
SD	0.8	0.9	0.6	0.6	0.7	0.4
<i>p</i> value	<i>p</i> <0.0001*	<i>p</i> <0.0001*	<i>p</i> =0.22	<i>p</i> =1.0	<i>p</i> =0.04*	<i>p</i> =0.004*

* Indicates significant *p*-values.

Table 2-4. Pearson correlation coefficients for stable carbon and oxygen isotope enamel ($\delta^{13}\text{C}_e$, $\delta^{18}\text{O}_e$) values and climatic and geographic variables.

	All Tapirs		<i>Tapirus bairdii</i>		<i>Tapirus terrestris</i>	
	$\delta^{13}\text{C}_e$ (VPDB, ‰)	$\delta^{18}\text{O}_e$ (VPDB, ‰)	$\delta^{13}\text{C}_e$ (VPDB, ‰)	$\delta^{18}\text{O}_e$ (VPDB, ‰)	$\delta^{13}\text{C}_e$ (VPDB, ‰)	$\delta^{18}\text{O}_e$ (VPDB, ‰)
Mean Monthly Temperature (°C)	-0.12	0.38*	-0.08	-0.47*	-0.31	-0.18
Precipitation Frequency (mean # of days per month)	-0.42*	0.05	-0.08	0.84*	-0.42	-0.38
Mean Monthly Precipitation (mm)	-0.50*	-0.03	0.13	0.63*	-0.56*	-0.61*
Latitude (absolute value)	0.47*	0.30	0.31	-0.36	0.78*	0.68*
Elevation (m)	0.19	-0.48*	-0.28	0.57*	0.45	0.34
$\delta^{18}\text{O}_{\text{precipitation}}$ (VSMOW, ‰)	-0.09	0.27	0.26	-0.76*	-0.04	0.06

* Indicates significant *p*-values.

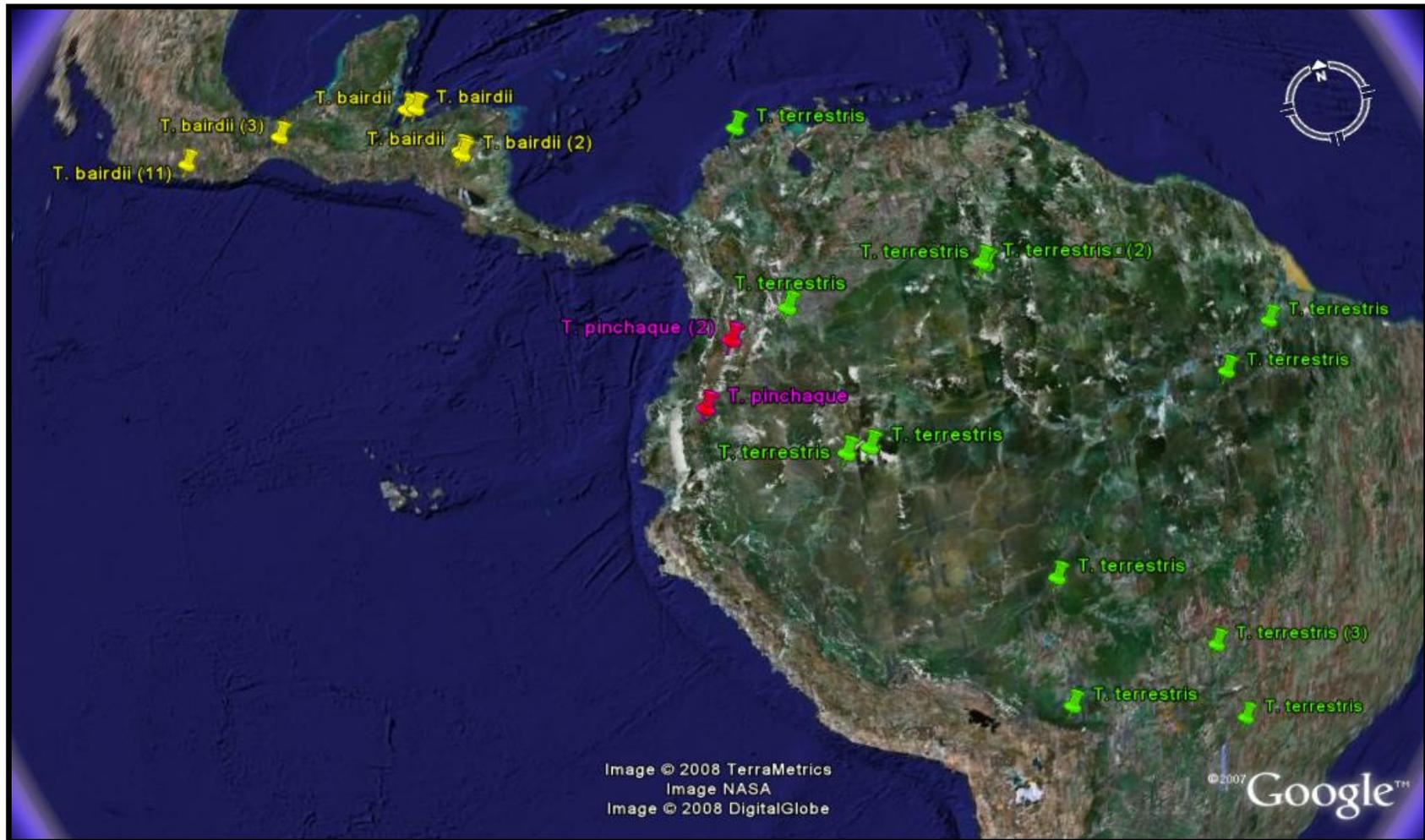


Figure 2-1. A Google Earth map showing the location of *Tapirus bairdii* (yellow), *Tapirus pinchaque* (purple), and *Tapirus terrestris* (green) specimens from southern Mexico, Central America, and South America. The numbers in parentheses indicate the number of specimens from one location (if greater than one).

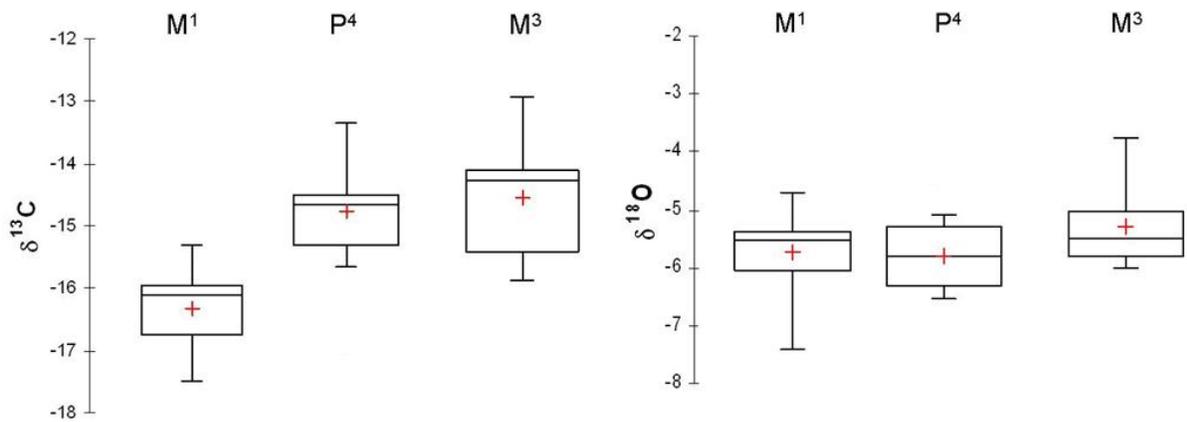


Figure. 2-2. Box plots of stable carbon and oxygen isotope values from a population of extant tapirs (*Tapirus bairdii*) in Acapulco, Mexico. Mean values and the total ranges of variation are noted by the red plus signs and bars, respectively. Tooth positions are noted in order of eruption timing (i.e. first molar, M1; fourth premolar, P4; and third molar, M3).

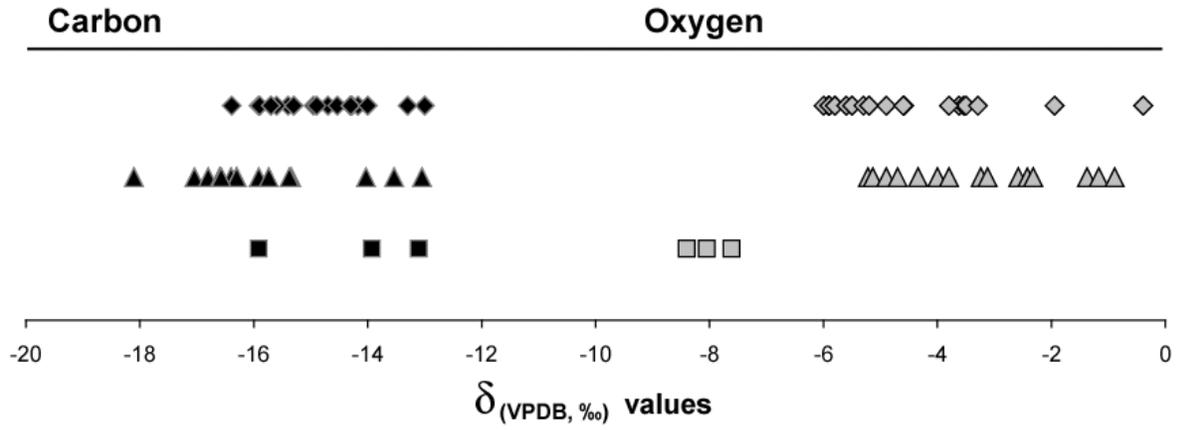


Figure. 2-3. Stable carbon (black) and oxygen (grey) isotope values of extant tapirs, *Tapirus bairdii* (diamonds), *Tapirus terrestris* (triangles), and *Tapirus pinchaque* (squares).

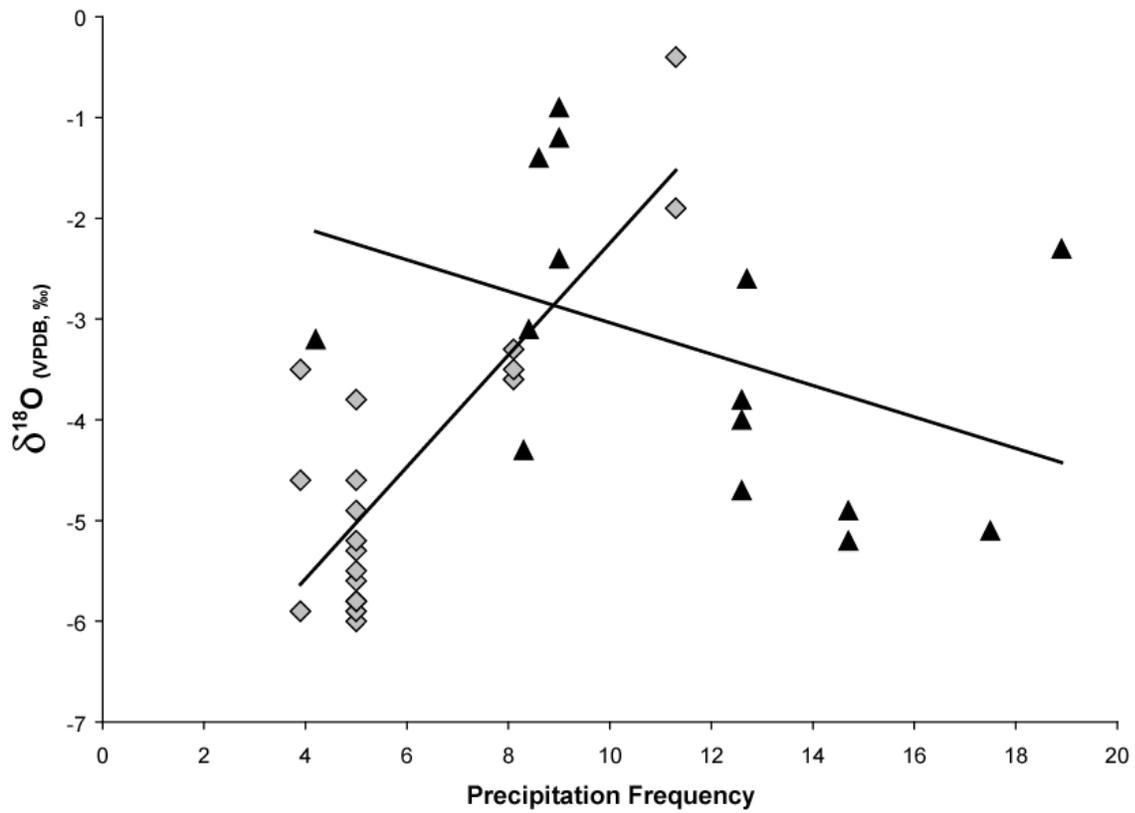


Figure 2-4. Relationships between precipitation frequency (mean number of precipitation days per month) and oxygen isotope values in *Tapirus bairdii* (diamonds; $y=0.55x-7.80$, $R^2=0.70$, $p<0.0001$) and *Tapirus terrestris* (triangles; $y=-0.15x-1.57$, $R^2=0.15$, $p=0.157$).

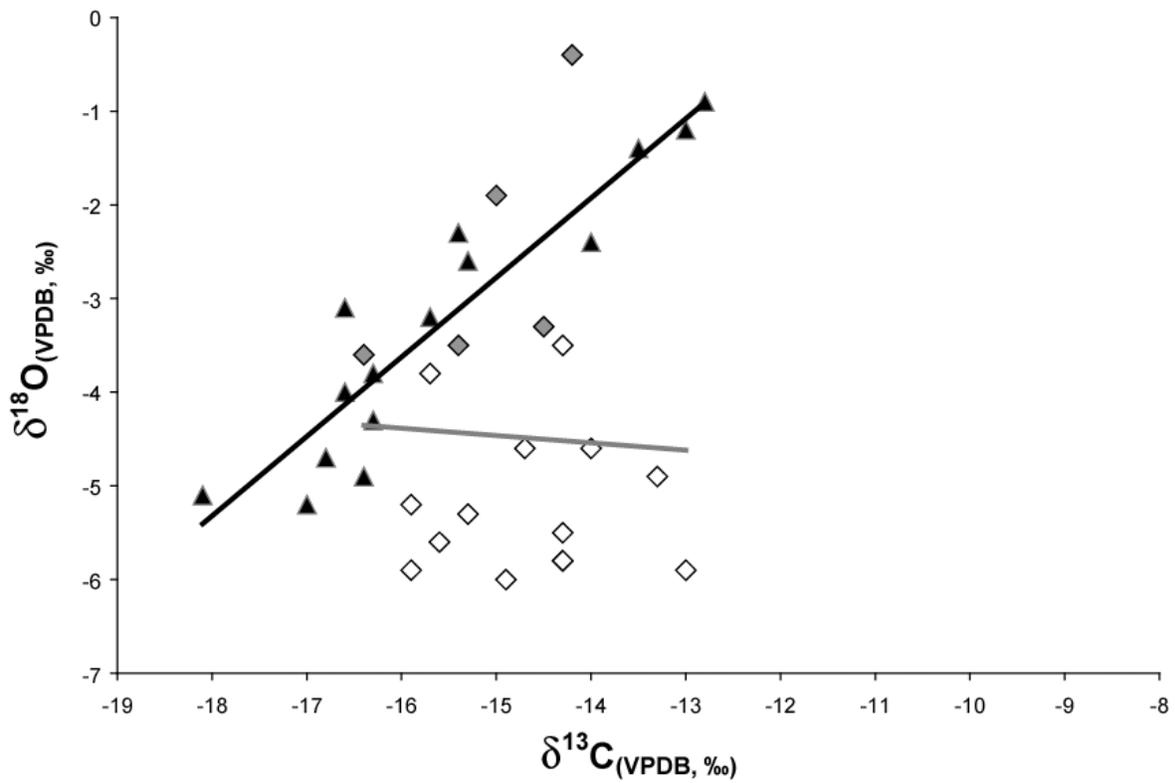


Figure 2-5. Relationship between carbon and oxygen isotope values from individual *Tapirus terrestris* (triangles; $y=0.85x+9.95$, $R^2=0.86$, $p<0.0001$) and *Tapirus bairdii* (diamonds; $y=-0.08x-5.63$, $R^2=0.002$, $p=0.85$) specimens, with grey diamonds indicating *T. bairdii* individuals present in areas with ≥ 5 precipitation days per month.

CHAPTER 3
NEOGENE FORESTS FROM THE APPALACHIANS OF TENNESSEE, USA:
GEOCHEMICAL EVIDENCE FROM FOSSIL MAMMAL TEETH

Introduction

Reconstructing the diet of ancient mammalian herbivores and their floral environment during the late Tertiary in eastern North America is necessary to understanding the context of mammalian evolution in this poorly understood region. Global climate change and C₃/C₄ transitions are interpreted to have taken place concurrently (Cerling et al., 1993, 1997; Wang et al., 1994). While these transitions lead to dramatic increases in C₄ grasses in North America approximately 7 mya (Cerling et al., 1993, 1997; Wang et al., 1994), it is unclear how eastern forests responded to such changes. It is possible that eastern North America sustained forest refugia, i.e. locations of relict populations of once widespread flora and fauna, during these transitions. The presence of a North American forest refugium has been proposed based on the Gray site's faunal and floral macrofossils including the abundance of forest-dwelling taxa (Wallace and Wang, 2004). Stable isotope sampling of the site's mammalian herbivores further clarifies our understanding of the paleoecology of this spatially and temporally rare site.

During the late Miocene to early Pliocene, herbivore diversity declined through a series of extinction events, with the once diverse short-crowned browsers experiencing proportionally greater declines than high-crowned (hypsodont), presumed grazing herbivores (Potts and Behrensmeyer, 1992; Janis et al., 2000, 2002, 2004). These declines are often attributed to the increase in C₄ grasslands resulting from increased aridity and/or reduced CO₂ levels globally (Potts and Behrensmeyer, 1992; Cerling et al., 1993, 1997; Wang et al., 1994; Janis et al., 2000, 2002, 2004; Retallack, 2001; Stromberg, 2005). While it is clear that C₄ grasses increased in abundance throughout the late Miocene to early Pliocene (Potts and Behrensmeyer, 1992; Cerling et al., 1993, 1997; Wang et al., 1994; Retallack, 2001), the driving mechanisms

responsible for apparent global cooling and increased seasonality are still a matter of debate. Nevertheless, it is possible that some forest environments may have persisted as floral and faunal refugia within or in close proximity to C₄ grasslands during this time of transition. As morphologically inferred browsers appear to be more numerous at the Gray site, it is important to understand the true dietary feeding strategies of all ungulate taxa present. Reconstructing the diets of ungulates will also provide information on the associated flora and likely environments of the Gray Fossil Site and the broader ramifications for the ancient Appalachian forests.

The southern Appalachians have existed for the past ~250 million years, potentially providing a relatively stable environment for the resident flora and fauna (Graham, 1964, 1999). Dominated by tropical flora during the Cretaceous the vegetation present during the Paleocene to early Eocene suggests tropical rain forests and a megathermal (i.e. humid and warm with mean temperatures of ≥ 20 °C, *sensu* de Candolle, 1874) climate (based on mesophyllous, entire-margined leaves in the Lower Eocene Wilcox Formation, TN). Middle Eocene tropical dry forests subsequently transitioned to modern warm-temperate deciduous vegetation at lower elevations and montane coniferous forests at higher elevations, during the late Tertiary (Graham, 1964, 1999). These late Tertiary flora consisted of tropical vegetation (at the genus and family level) that were adapted to more temperate climates and interchanged with Asia and Europe (Graham, 1964). Additionally, molecular evidence of extant flora and fauna (e.g. eastern tiger salamander *Ambystoma tigrinum tigrinum*, red pine *Pinus resinosa*) suggests that southern Appalachian refugia maintained ancestral population of taxa, requiring milder climates, during periods of glaciations (Crespi et al., 2003; Walter et al., 2005). Thus, understanding the paleoecology of the southern Appalachians may help us to better understand present floral and faunal diversity.

The primary objective of this study is to reconstruct the ancient diets and paleoenvironments from the fauna of the Gray Fossil Site, from stable carbon and oxygen isotopes of ungulate tooth enamel. I also interpret the paleoclimatic records of serial samples from tooth and tusk enamel, determining seasonal variability. Additionally, I present Rare Earth Element (REE) analyses of a subset of our ungulate taxa to determine the taphonomic context of the mammalian herbivores, determining if they represent a sympatric fauna (Trueman, 1999). The results of this study provide critical information to understanding the unique paleoecological dynamics occurring during the late Tertiary in the southern Appalachians.

Background

Stable Isotope Analysis: A Theoretical Foundation

Vertebrate fossil remains can clarify paleoecological hypotheses by allowing for an independent measure of habitat type, as inferred from stable isotope ratios. Stable carbon isotopes are incorporated into the lattice of enamel hydroxyapatite; therefore, retaining dietary isotopic signals that are reflective of plants consumed (DeNiro and Epstein, 1978; Krueger, 1991; Lee-Thorp and van der Merwe, 1991; Cerling et al., 1997; Cerling and Harris, 1999). Because $^{13}\text{C}/^{12}\text{C}$ ratios vary depending on a plant's photosynthetic pathway and do not decay with time (Ehleringer and Monson, 1993), the ratios of the past can be interpreted as similar to those of today (Cerling et al., 1997). Additionally, $\delta^{13}\text{C}$ signatures of C_3 and C_4 plants are incorporated into the tooth enamel hydroxyapatite of medium to large bodied herbivorous mammals with an enrichment factor of 14.1‰ (although non-ruminants may have an enrichment factor between 12 and 13‰; Cerling and Harris, 1999). However, due to modern atmospheric CO_2 enrichment, floral and faunal $\delta^{13}\text{C}$ values are an additional $\sim 1.5\%$ enriched today, as compared to the past (Cerling et al., 1997; Passey et al., 2002). Therefore, $\delta^{13}\text{C}$ values between -21% and -7% reflect a C_3 diet, whereas values between -2% and 4% indicate a C_4 diet

(MacFadden et al., 1996; Cerling et al., 1997, 1999, 2004; Cerling and Harris, 1999). Variation in $\delta^{13}\text{C}$ values within individual teeth can also indicate seasonal differences in diet, reflective of seasonal changes in vegetation due to water stress (Roux et al., 2001; Ehleringer et al., 2002).

Stable carbon isotope data of extinct and extant taxa can also be used to reconstruct rainforest distributions due to greater ^{13}C discrimination occurring in dense closed canopies as compared to more open C_3 environments (van der Merwe and Medina, 1989; Cerling et al., 2004). Because $\delta^{13}\text{C}$ values increase with decreasing canopy density and/or increasing distance from dense forest edges (van der Merwe and Medina, 1989; Kapos et al., 1993; West et al., 2001), more negative $\delta^{13}\text{C}_{\text{enamel}}$ values of mammalian herbivores reflect the consumption of browse in forests with denser canopies (van der Merwe and Medina, 1989, 1991; Cerling et al., 2004). As temperate forest floral $\delta^{13}\text{C}$ values are typically more enriched in ^{13}C as compared to tropical forests (e.g. Cerling et al., 2004; Tu et al., 2004; BASIN Network, 2006), floral macrofossils and palynological evidence can further constrain interpretations of forest density. Therefore, $\delta^{13}\text{C}$ values of mammalian tooth enamel can indicate meaningful differences in habitat type within C_3 flora and therefore assist in determining relative canopy density.

Variation in stable oxygen isotopes of mammalian tooth enamel is a function of body water that reflects the response of meteoric water to changes in temperature and/or precipitation/humidity (Dansgaard, 1964; Bryant et al., 1994, 1996a,b,c; Bocherens et al., 1996; Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999; Higgins and MacFadden, 2004; MacFadden and Higgins, 2004; Hoppe, 2006). In terrestrial ecosystems, seasonal variation is recorded in tooth enamel with more positive $\delta^{18}\text{O}$ values indicating high summer temperatures as compared to more negative $\delta^{18}\text{O}$ values during cooler winters (Fricke and O'Neil, 1996; Feranec and MacFadden, 2000; MacFadden and Higgins, 2004).

Oxygen isotopes of mammalian tooth enamel can also vary between taxa occupying similar environments due to variations in the proportion of water ingested in the form of drinking water, as opposed to more evaporated plant water (Levin et al., 2006). By comparing the $\delta^{18}\text{O}$ values of evaporation sensitive taxa (i.e. $\delta^{18}\text{O}_{\text{enamel}}$ values increase with aridity) to evaporation insensitive taxa (i.e. $\delta^{18}\text{O}_{\text{enamel}}$ values track meteoric water) present at the same site, the $\delta^{18}\text{O}$ values of mammalian tooth enamel may be used as an index of terrestrial aridity (Levin et al., 2006). Because rhinos are evaporation insensitive (Levin et al., 2006), comparisons of the $\delta^{18}\text{O}$ values of rhinos to the likely evaporation sensitive camels (i.e. non-domesticated camelids typically acquire a large proportion of their water from plants), may elucidate relative aridity at the Gray site.

Rare Earth Element Analysis: Understanding Taphonomic History

REE patterns of fossilized skeletal material within a deposit can be compared to determine whether a site has experienced significant mixing and/or reworking (Trueman, 1999). Because REEs are taken up in skeletal tissue in higher concentrations beginning shortly after death and continuing for approximately 10,000 to 30,000 years during diagenetic recrystallization, REEs patterns of fossil enamel and dentin reflect the geochemistry of the local pore-water during that time (Henderson et al., 1983; Trueman, 1999; Patrick et al., 2001; MacFadden et al., 2007). As early recrystallization results in reduced porosity and flow, initial REE patterns are typically preserved throughout latter diagenesis (Trueman, 1999). Similar REE patterns indicate similarities in the geochemistry of the pore-water, and comparable depositional environments (Trueman, 1999; Trueman et al., 2004). Therefore, it is possible to compare REE patterns of fossils from the Gray site to determine if they shared similar depositional environments or were reworked from a spatially and/or temporally distinct locality.

Gray Fossil Site, Tennessee, USA

The Gray Fossil Site, located in Washington, Co., Tennessee, USA (Figure 3-1) is biostratigraphically dated between 4.5 and 7 Ma, based on the presence of the rhino *Teleoceras* and short faced bear *Plionarctos* (Wallace and Wang, 2004). The site is a sinkhole deposit consisting of finely laminated clays, silts, and fine sands with intermixed gravel lenses. The deposit resulted from a paleosinkhole lake that was approximately 2 ha in size and up to 39 m thick (Wallace and Wang, 2004; Shunk et al., 2006). The vertebrate taxa are of North American and, somewhat surprisingly, Eurasian ancestry (Table 3-1). The ungulate taxa include, the tapir *Tapirus polkensis*, rhino *Teleoceras* cf. *T. hicksi*, camel cf. *Megatylopus* sp., peccary Tayassuidae, and gomphotheriid proboscidean (Table 3-1). Additionally, the Gray site preserves a large population of the extinct tapirs (*Tapirus polkensis*) represented by over 70 individuals, an order of magnitude larger than the total number of individuals of all other ungulate taxa. Given that fossil tapirs are robust indicators of ancient forests (DeSantis and MacFadden, 2007), the Gray site likely indicates the presence of forest environments.

Floral macrofossils and pollen likewise support a forest interpretation for the Gray site. Palynological evidence suggests a predominantly oak (*Quercus*) and hickory (*Carya*) forest, consisting of nearly 70% of the pollen (Wallace and Wang, 1994; Table 3-1). Along with pine (*Pinus*), representing 9% of the pollen analyzed, the remaining flora present occurs in even lower abundances (Wallace and Wang, 1994). Because grass pollen occurs in such low abundance (< 2%), and anemophilous (wind dispersed) grass pollen is often over representative of a sites flora when present (Horrocks et al., 2000), it is unlikely that C₄ grasses made up a substantial portion of the vegetation present at the Gray site. Additionally, the $\delta^{13}\text{C}$ values of all bulk organic matter sampled from the site range in value from -28 to -24‰, representing only C₃ flora (Shunk et al., 2006).

Materials and Methods

Morphological Measurements

Selected dental measurements were taken to quantify relative crown height. Measurements of crown heights and widths of the lower third molars (m3) were taken from all specimens isotopically sampled with m3s present. A hypsodonty index (HI) was then calculated for all available m3s according to Janis (1988), by dividing the unworn crown height by the m3 width. Lower third molars with significant wear were excluded when determining mean HI values. These HI values were then used to determine if hypsodonty is predictive of diet, as inferred from stable carbon isotopes at the Gray Fossil Site.

Stable Isotope Analysis

A total of 32 bulk and 58 serial enamel samples from 32 individuals were analyzed from the Gray Fossil Site in eastern Tennessee (Table 3-1, 3-5). Samples were primarily collected from late erupting teeth (i.e. third molars or fourth premolars) in order to avoid sampling teeth that mineralized while nursing or weaning. Bulk samples were collected from one area parallel to the growth axis of the tooth. Serial samples were acquired by sampling the teeth with parallel grooves at intervals of 2-3 mm perpendicular to the growth axis of the tooth. When sampling the gomphothere tusk, a total of 14 samples, each 1.5 mm wide in the growth direction and 15 mm across the enamel band, were taken every 5 mm in order to acquire data representative of at least one year of growth (Fox and Fisher, 2004). Between 2-10 mg of tooth enamel sample was collected using a low speed FOREDOM™ dental drill and carbide dental burrs. Samples were chemically pretreated prior to isotopic analysis with H₂O₂ to remove organics and weak acetic acid (0.1N, CH₃CO₂H) to remove secondary carbonates (Koch et al., 1997). Approximately 1 mg of treated sample was then analyzed using a VG Prism mass spectrometer in the Department of Geological Sciences at the University of Florida.

Stable isotope data are reported in conventional delta (δ) notation for carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$), where $\delta^{13}\text{C}$ (parts per mil, ‰) = $((R_{\text{sample}}/R_{\text{standard}})-1)*1000$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$; and, $\delta^{18}\text{O}$ (parts per mil, ‰) = $((R_{\text{sample}}/R_{\text{standard}})-1)*1000$, and $R = {}^{18}\text{O}/{}^{16}\text{O}$. Analyzed samples were calibrated to NBS-19 and then to V-PDB (PeeDee Belemnite) following the Vienna (V-) convention (Coplen, 1994).

Rare Earth Elemental Analysis

Enamel and dentin from the gomphothere tusk, 1 rhino tooth, and 3 tapir teeth (each from different individuals), were sampled for REE analysis. Approximately 5-10 mg of sample was removed using a FOREDOM™ dental drill and carbide dental burrs. These samples were cleaned in Savillex™ vials with 1 ml of 3 M HNO_3 , dissolved and heated overnight on a hot plate. After samples were dried until all liquid was evaporated, the samples were weighted and dissolved in 2 ml of 5% HNO_3 and left overnight on a hotplate. Approximately 3 ml of 5% HNO_3 was added to each sample and the sample weights were calculated in order to achieve a dilution factor of 2000. All samples were then run on a Thermo Finnigan ELEMENT2 inductively Coupled Plasma Mass Spectrometer in the University of Florida Department of Geological Sciences for bulk REE concentrations. Internal standards and bone ash (NVS SRM 1400) were run with the samples, enabling corrections to be made due to instrument drift. All REE concentrations were normalized to PAAS (Post-Archean Australian Shale; McLennan, 1989). The REEs analyzed, range from La ($Z = 57$) to Lu ($Z = 71$). We excluded europium (Eu) from the analysis *post hoc*, due to anomalous Eu enrichment and depletion spikes found in the Gray specimens. These anomalies are likely due to Eu partitioning under closed conditions and irrelevant for our comparisons (Trueman et al., 2004). These methods follow Trueman et al. (2004) and MacFadden et al. (2007).

Results and Discussion

Bulk Carbon Isotope Analysis

The bulk carbon isotopic analyses of *Tapirus polkensis* indicates a diet consisting entirely of C₃ plants ranging in $\delta^{13}\text{C}$ values from -14.1 to -10.9‰ with a mean of -13.0‰ ($1\sigma = 0.9\text{‰}$; Figure 3-2, Table 3-2 and 3-3). The bulk $\delta^{13}\text{C}$ values of *Teleoceras* sp., a morphologically presumed grazer (MacFadden, 1998), range from -13.6 to -13.0‰ with a mean of -13.3‰ ($1\sigma = 0.3\text{‰}$; Figure 3-2, Table 3-2 and 3-3). Peccary (Tayassuidae) bulk $\delta^{13}\text{C}$ values range from -14.0 to -12.4‰ , with a mean of -13.1‰ ($1\sigma = 0.8\text{‰}$; Figure 3-2, Table 3-2 and 3-3). These taxa are therefore interpreted to be obligate browsers, consuming only C₃ vegetation. While only one tooth was available for isotopic analysis of the camel, cf. *Megatylopus* sp., the $\delta^{13}\text{C}$ value of -13.8‰ is consistent with a predominantly C₃ diet (Figure 3-2, Table 3-2 and 3-3). The carbon isotopic niches of *Tapirus*, *Teleoceras*, the peccary and the camel appear to overlap and are not statistically different from each other (ANOVA, $p = 0.81$; Kruskal-Wallis, $p = 0.79$; Figure 3-2), although it is difficult to comment on the degree of niche overlap due to the limited number of *Teleoceras*, peccary, and camel teeth sampled. The bulk $\delta^{13}\text{C}$ value of the tusk from the gomphotheriid proboscidean is -0.3‰ (Figure 3-2, Table 3-2 and 3-3), significantly different from all other taxa sampled under parametric analyses of ANOVA ($p < 0.0001$) and all subsequent Fisher LSD multiple comparisons ($p < 0.05$). However, non-parametric Kruskal-Wallis analysis yielded insignificant differences ($p = 0.44$), likely because the gomphotherid tusk represents only one sample. This inconsistent $\delta^{13}\text{C}$ value prompted a comparison of enamel and dentin REEs from the proboscidean with those of the tapirs and rhinos. This analysis, discussed later, enabled me to determine if the tusk was subjected to a similar depositional environment as the more abundant forest-dwelling taxa (i.e. *Tapirus* and *Teleoceras*).

As prior pollen analyses have identified the Gray Fossil Site to indicate a predominantly oak-hickory deciduous forest, we can constrain our interpretation of canopy density. Average $\delta^{13}\text{C}$ values of modern temperate deciduous flora of approximately -26‰ and -30‰ are consistent with an open forest canopy and dense forest canopy, respectively (Garten and Taylor, 1992; Tu et al., 2004; BASIN Network, 2006). Accounting for both dietary (14.1‰ enrichment between large bodied ungulates and their diet; Cerling and Harris, 1999) and atmospheric enrichment (1.5‰; Cerling et al., 1997; Passey et al., 2002), all taxa with the exception of the proboscidean have mean $\delta^{13}\text{C}$ values consistent with a moderately dense, temperate forest ($\delta^{13}\text{C} \sim -13\text{‰}$). The bulk $\delta^{13}\text{C}$ values from the tapirs, rhinos, peccaries, and the camel do not support the presence of C_4 grasses at the Gray site. These data agree with the palynological evidence that documents low grass abundance (Wallace and Wang, 2004), of which the Gramineae pollen that is present may be from C_3 grasses. However, the bulk $\delta^{13}\text{C}$ value from the gomphothere indicates the presence of C_4 grasses at a distance within this species migration/home range and in large enough abundance to support a population of this herbivore with a pure C_4 diet, assuming that our gomphothere sample is representative of a population. Given that roughly contemporaneous sites below 37° latitude are thought to have undergone transitions to C_4 grasslands during the late Miocene/early Pliocene (Cerling et al., 1993, 1997; Wang et al., 1994), these data presented here suggest the presence of a forest environment at the Gray Fossil Site that may have served as a refugium to taxa requiring forest habitats among C_4 grasslands.

The relationship between relative tooth crown height (hypsodonty index values) and $\delta^{13}\text{C}$ values are explored here. The average HI values of *Tapirus*, *Teleoceras*, and peccaries are 0.7, 1.3, and 0.5, respectively. Because the sample sizes of rhinos and peccaries are small, these HI values should be viewed as preliminary. These HI values are not predictive of $\delta^{13}\text{C}$ values.

Instead, the most hypsodont taxon *Teleoceras* has some of the most negative $\delta^{13}\text{C}$ values. While high-crowned teeth are no longer synonymous with the grazing of C_4 grasses (MacFadden et al., 1999; Feranec, 2003, 2004; MacFadden, 2005), the Gray fauna likewise provides additional evidence that hypsodont teeth do not indicate C_4 grazing. Additionally, the browsing of C_3 vegetation by the high-crowned *Teleoceras*, a morphologically presumed grazer and isotopically classified mixed feeder/ C_4 grazer in Florida during the early Miocene (MacFadden, 1998), demonstrates further support of the absence of significant C_4 flora at the Gray site.

Bulk Oxygen Isotope Analysis

Bulk $\delta^{18}\text{O}$ values of *Tapirus polkensis* range from -5.2 to -2.3‰ with a mean of -4.0‰ ($1\sigma = 0.7\text{‰}$; Figure 3-2, Table 3-2 and 3-3), not significantly different from *Teleoceras*, peccaries, and the gomphothere (ANOVA, $p = 0.15$; Kruskal-Wallis, $p = 0.21$). The bulk $\delta^{18}\text{O}$ values of *Teleoceras* sp. range from -5.5 to -3.9‰ with a mean of -4.8‰ ($1\sigma = 0.7\text{‰}$), this is the most negative mean $\delta^{18}\text{O}$ value of all ungulates sampled (Figure 3-2, Table 3-2 and 3-3). The bulk $\delta^{18}\text{O}$ values of the peccaries range from -4.9 to -4.1‰ with a mean of -4.4‰ ($1\sigma = 0.4\text{‰}$; Figure 3-2, Table 3-2 and 3-3). Additionally, the bulk $\delta^{18}\text{O}$ value of the gomphothere tusk falls within the range of the tapirs, rhinos, and peccaries at -4.2‰ . The $\delta^{18}\text{O}$ of -1.7‰ for the camel (cf. *Megatylopus* sp.) is the most enriched in ^{18}O (Figure 3-2, Table 3-2 and 3-3), significantly different from all other taxa sampled under parametric analyses of ANOVA ($p < 0.01$) and LSD multiple comparisons ($p \leq 0.01$). No significant differences are observed when using the non-parametric Kruskal-Wallis analysis ($p = 0.13$); however, this is likely a sample size issue because only one camel tooth is included in the analysis. The highly enriched $\delta^{18}\text{O}$ value from the camel, a probable evaporation sensitive taxon, may be compared to evaporation insensitive rhinos to quantify relative aridity (Levin et al., 2006). *Teleoceras* has the most depleted bulk $\delta^{18}\text{O}$ value of -5.5‰ and the camel has the most enriched $\delta^{18}\text{O}$ value of -1.7‰ ;

therefore, the total bulk $\delta^{18}\text{O}$ range of all taxa is 3.8‰. Comparing the difference between the evaporation insensitive rhino and likely evaporation sensitive camel may further allow for estimates of relative aridity (Levin et al., 2006); however, additional samples of both the evaporation insensitive and sensitive taxa are first needed.

Seasonal Reconstructions: Serial Sample Analysis

The serial samples of *Teleoceras*, *Tapirus* and peccary teeth can reveal seasonal differences in monthly temperatures and/or precipitation. *Teleoceras* serial samples ($N = 12, 14$) from two high-crowned teeth yield total $\delta^{13}\text{C}$ ranges of 0.6‰ (−13.7 to −13.1‰) and 1.0‰ (−13.7 to −12.7‰), with $\delta^{18}\text{O}$ ranges of 1.1‰ (−6.1 to −5.0‰) and 1.3‰ (−5.1 to −3.8‰; Figure 3-3B, Table 3-4, 3-5). Serial samples from two tapir individuals ($N = 8, 6$), yield total $\delta^{13}\text{C}$ ranges of 1.1‰ (−12.3 to −13.4‰) and 1.3‰ (−10.6 to −11.9‰), with $\delta^{18}\text{O}$ ranges of 1.1‰ (−3.9 to −2.8‰) and 0.8‰ (−3.6 to −2.8‰; Figure 3-3A, Table 3-4, 3-5). One peccary tooth ($N = 4$) was sampled to determine if it demonstrates the same pattern of little $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variation. The range of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variation was 0.6‰ (−12.6 to −13.2‰) and 1.4‰ (−5.6 to −4.2‰), respectively (Figure 3-3A, Table 3-4, 3-5). All serial samples of *Teleoceras*, *Tapirus*, and the peccary demonstrate less than 1.5‰ variation in both carbon and oxygen isotopes, indicating the lack of significant seasonal variation.

Serial samples of the gomphothere tusk ($N = 14$) were taken at intervals representing over one year of growth (as per Fox and Fisher, 2004), varying ≤ 1 ‰ in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. The gomphothere $\delta^{13}\text{C}$ values ranged from −0.7 to 0.3‰ (Figure 3-3C, Table 3-4, 3-5), indicating the consumption of C_4 grass throughout the course of a year with the absence of seasonal variations in diet. The lack of significant oxygen variation (approximately 0.6‰, −4.6 to −4.0‰) likewise confirms the lack of significant seasonal changes in meteoric water due to temperature and/or precipitation. The variation of tusk $\delta^{13}\text{C}$ seen here is similar to late Miocene

gomphotheres with equable serial sample records of approximately 1‰; however, those gomphotheres were C₃ browsers and/or mixed feeders (Fox and Fisher, 2001, 2004; Figure 3-3C). The absence of considerable δ¹³C and δ¹⁸O variation is consistent with the isotopic patterns found in the tooth enamel of the ungulates sampled. However, the lack of seasonal variation may be an artifact of the gomphothere's behavior, if it actively migrated to areas where C₄ grasses were abundant (i.e. migrating south during the winter to consume C₄ grasses under similar temperature/precipitation conditions as summer grazed C₄ grasses of northern latitudes). Additionally, we can not infer that the gomphothere only consumed C₄ vegetation during its life including while at or near the Gray Fossil site. Instead, we can only state that the gomphothere sampled consumed a diet indicative of a pure C₄ diet for at least one year of its life.

The lack of significant variation in both the carbon and oxygen isotopes from all taxa sampled, suggests minor differences in monthly temperatures and/or precipitation during the Neogene in eastern Tennessee. The Gray fauna experienced a more equable climate than today (Climate Zone, 2006; U.S. Department of Commerce and NOAA, 2006; Waterisotopes.org, 2006; Figure 3-4). Even though δ¹⁸O variation is damped in mammalian tooth enamel due to the buffering of water sources and/or time averaging (Passy and Cerling, 2002), the *Teleoceras*, *Tapirus*, and peccary δ¹⁸O ranges of variation are more similar to fossil taxa from the aseasonal Gaillard Cut Local Fauna assemblage in Panama (MacFadden and Higgins, 2004; Figure 3-3A and 3-3B), than to taxa from highly variable climates. The serial samples of the rhinos *Floridaceras whitei* from the 15-million-year-old site in Panama have δ¹³C variation of 0.5‰ (MacFadden and Higgins, 2004), similar to 0.7‰ and 1.0‰ of *Teleoceras* from the Gray site (Figure 3-3B, Table 3-4). However, the δ¹⁸O variation of 1.6‰ and 1.8‰ for *Floridaceras* from the Gaillard Cut L.F. (MacFadden and Higgins, 2004) appears greater than the range of 1.1‰

and 1.2‰ in *Teleoceras* (Figure 3-3B, Table 3-4). Additionally, annual variation in carbon and oxygen isotope values can yield differences as great as 4‰ in tooth enamel of taxa that are present in seasonally variable climates (as seen in bison, horses, and mammoths in Feranec and MacFadden, 2000); therefore, variation of < 1.5‰ supports a relatively aseasonal climate (with regard to precipitation and/or temperature). Despite the presence of a deciduous temperate flora that are typically present in highly seasonal environments, the limited range of variation between serial samples likely represents a warmer and less seasonally variable climate than currently present in modern eastern North American temperate forests. Therefore, the floral environment of the Gray site may resemble more equable broadleaf forests than those present in the Appalachians today.

Evidence of a Forest Refuge

REE analysis of the gomphothere tusk, and *Tapirus* and *Teleoceras* teeth allow for a comparison of patterns of REEs obtained post-mortem. Normalized REE patterns of enamel and dentin from the gomphothere tusk are nearly identical to, and closely parallel, those of sampled enamel and dentin from *Tapirus* and *Teleoceras*, despite differences in concentrations of REEs (Figure 3-5). Because similar REE patterns indicate comparable depositional environments (Trueman, 1999), it is likely that the tusk was deposited at the Gray site at a similar time to the rhinoceros and tapirs sampled for REEs, as opposed to being reworked. Therefore, the gomphothere's REE patterns indicate that it died at or in close proximity to the Gray Fossil Site.

The bulk and serial $\delta^{13}\text{C}$ values of the gomphothere tusk provide conclusive evidence that C_4 grasses were at least present within a distance no larger than the migration/home range of the individual sampled. While we are unable to determine the home range of gomphotheres or if they migrated, using modern proboscideans as analogues migration/home ranges may have been as large as 7000 km^2 (Stuwe et al., 1998). Therefore, C_4 grasses may have been present adjacent

to the Gray site or at the fringes of the gomphothere's home range, potentially hundreds of kilometers away. As our gomphothere did consume a primarily C₄ diet over the course of at least one year, it is likely that C₄ grasses occurred in abundances large enough to support both itself and a population of gomphotheres with pure C₄ diets, if our gomphothere's diet is representative of a population. While the gomphothere sampled has anomalous $\delta^{13}\text{C}$ values in relation to its browsing adapted dentition, gomphotheres have been described as isotopically inferred mixed C₃/C₄ feeders and C₄ grazers, in addition to C₃ browsers (MacFadden and Shockey, 1997; Cerling et al., 1999; Sánchez et al., 2003, 2004; Todd et al., 2006). Because the bulk $\delta^{13}\text{C}$ values from the tapirs, rhinos, peccaries, and the camel do not support the presence of C₄ grasses at the Gray site and palynological evidence indicates the low abundance of grass pollen (Wallace and Wang, 2004), it is improbable that C₄ grasses were present at significant levels at the site. Instead, the Gray Fossil Site likely represents a forest environment that may have served as a refuge to taxa in the southern Appalachians requiring C₃ browse, present concurrently with C₄ grasslands. The presence of forest dwelling taxa such as the tapirs and red panda (*Pristinailurus bristoli*) at the Gray site demonstrates additional support that this forest environment may have provided unique habitat to taxa that were more widespread previously.

Conclusions

The mammalian herbivores from the Gray Fossil Site provide evidence of moderately dense ancient forests, flanked by distal C₄ grasslands. Both bulk and serial carbon isotopes indicate that all ungulate taxa sampled, with the exception of the gomphothere, consumed a diet of C₃ vegetation. Because all of the $\delta^{13}\text{C}$ values of *Tapirus*, *Teleoceras*, the peccaries, and the camel are less than -10‰, there is no isotopic evidence that suggests the consumption of C₄ grasses by these taxa. Therefore, the Gray site represents a forest environment large enough to support sustainable populations of its browsers (tapir *Tapirus polkensis*, rhino *Teleoceras* cf. *T.*

hicksi, camel cf. *Megatylopus* sp., peccary Tayassuidae). The majority (63%) of specimens sampled have depleted $\delta^{13}\text{C}$ values of $\leq -13\text{‰}$, further suggesting that this dominant oak-hickory forest had a relatively dense canopy for a temperate forest.

The presence of organisms that currently live in humid mesothermal (i.e. moderate moisture and heat with mean temperatures between 15-20 °C, *sensu* Wolf 1975 modified from de Candolle 1874) and/or megathermal areas such as tapirs and alligators provides evidence for a warmer and more equable climate than today. Serial samples of tooth and tusk enamel document $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variation of $< 1.5\text{‰}$, demonstrating negligible seasonal changes in temperature and/or precipitation. Assuming that the climate was warmer (as inferred from the taxa present) and that the relatively constant annual precipitation patterns seen today (Sankovski and Pridnia, 1995; Climate Zone, 2006; U.S. Department of Commerce and NOAA, 2006; Figure 3-4) occurred in the past, we would expect to see minor differences in $\delta^{18}\text{O}$ values. Additionally, relatively constant precipitation and warmer mean annual temperatures could explain why C_3 and C_4 floras do not experience seasonal water stress (as inferred from the lack of seasonally enriched $\delta^{13}\text{C}$ values), due to greater evaporation during periods of increased temperature and/or aridity. Currently, the southern Appalachians are relatively warm and humid at low elevations, while precipitation shows little seasonality. Therefore, the Gray site may have served as a refugium to taxa requiring C_3 vegetation and more equable/warmer environments than may have been available at other geographical localities during the Miocene/Pliocene C_4 grassland transition.

Due to limited numbers of *Teleoceras*, peccary, and camel specimens sampled, it is too early to speculate on the true degree of niche overlap present at this site. Continued excavation of the Gray Fossil Site will provide larger samples from which future analyses of isotopic niche

overlap can be clarified. Additionally, microwear analysis of the ungulates sampled isotopically will provide further resolution to whether C_3 consumers were feeding on C_3 grasses and/or C_3 browse. The continued sampling of the vertebrate fauna present at the Gray site will further clarify ecological niches and seasonal variation. In particular, additional gomphothere samples will shed light on population level dietary variation including estimates of percent C_4 grass consumption. These mammalian herbivores from the Neogene of eastern North America provide unique opportunities to understand paleoecological phenomenon occurring during a period of dramatic global change.

Table 3-1. Biota from the Gray Fossil Site, Tennessee. Compiled from Wallace and Wang (2004) and Schubert and Wallace (2006).

Fauna	Flora
Osteichthyes	Conifers
Amphibia	<i>Pinus</i>
Anura	<i>Tsuga</i>
Plethodontidae	Deciduous
<i>Ambystoma</i> sp.	<i>Quercus</i>
Reptilia	<i>Carya</i>
<i>Chrysemys</i> sp.	<i>Ulmus</i>
<i>Trachemys</i> sp.	<i>Betula</i>
<i>Terrapene</i> sp.	<i>Fraxinus</i>
Chelydridae	<i>Celtis</i>
<i>Alligator</i> sp.	Shrubs
Viperidae	<i>Alnus</i>
Colubridae	<i>Salix</i>
Aves	Herbs
Passeriformes	<i>Ambrosia</i> -type
Mammalia	Cyperaceae
Soricidae	Gramineae
Talpidae	Umbelliferae
Lagomorpha	Caryophyllaceae
Rodentia	
Xenarthra	
Gomphotheriidae	
<i>Tapirus polkensis</i>	
<i>Teleoceras</i> cf. <i>T. hicksi</i>	
Tayassuidae	
cf. <i>Megatylopus</i> sp.	
Canidae	
Mustelidae	
cf. <i>Machairodus</i> sp.	
<i>Plionarctos</i> sp.	
<i>Pristina ilurus bristoli</i>	
<i>Arctomeles dimolodontus</i>	

Table 3-2. Bulk carbon and oxygen isotopes of mammalian ungulate enamel, Gray Fossil Site, Tennessee.

Taxon	Specimen No.*	Tooth Position	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
<i>Tapirus polkensis</i>	291	LM2	-13.0	-3.7
<i>T. polkensis</i>	586	partial RP4,M2,or M3	-13.9	-3.8
<i>T. polkensis</i>	587	partial LP4,M2,or M4	-12.7	-3.5
<i>T. polkensis</i>	588	Rm3	-13.7	-4.2
<i>T. polkensis</i>	595	Lm3	-13.1	-2.8
<i>T. polkensis</i>	602	Lp4	-12.1	-4.5
<i>T. polkensis</i>	606	LM3	-13.4	-4.2
<i>T. polkensis</i>	607	RM3	-13.3	-4.1
<i>T. polkensis</i>	608	RM3	-11.2	-4.3
<i>T. polkensis</i>	623	RM3	-14.1	-4.6
<i>T. polkensis</i>	639	LM2	-12.7	-4.2
<i>T. polkensis</i>	652	RM2	-13.1	-4.5
<i>T. polkensis</i>	653	LM3	-14.0	-4.6
<i>T. polkensis</i>	661	LM2	-13.9	-2.3
<i>T. polkensis</i>	664	RM3	-11.5	-3.9
<i>T. polkensis</i>	666	LM3	-14.0	-5.2
<i>T. polkensis</i>	683	LM3	-13.7	-4.1
<i>T. polkensis</i>	3424	RM3	-12.9	-3.8
<i>T. polkensis</i>	3425	RM3	-13.4	-4.5
<i>T. polkensis</i>	3426	LM2	-13.7	-3.0
<i>T. polkensis</i>	3427	LM2	-13.6	-4.1
<i>T. polkensis</i>	2/20/04-027	Lm3	-10.9	-3.4
<i>T. polkensis</i>	2002-5-119	LM3	-12.4	-4.7
<i>Teleoceras</i> cf. <i>T. hicksi</i>	566	Rp3	-13.4	-3.9
<i>Teleoceras</i> cf. <i>T. hicksi</i>	609	Lm3	-13.2	-5.5
<i>Teleoceras</i> cf. <i>T. hicksi</i>	780	RM1	-13.0	-4.6
<i>Teleoceras</i> cf. <i>T. hicksi</i>	781	LM1	-13.6	-5.3
Tayassuidae	593	LM3	-14.0	-4.2
Tayassuidae	778	LM3	-12.4	-4.1
Tayassuidae	779	Rm3	-12.9	-4.9
cf. <i>Megatylopus</i> sp.	738	deciduous premolar	-13.8	-1.7
Gomphotheriidae	305	tusk	-0.3	-4.2

* All specimen numbers are East Tennessee Museum of Natural History catalogue numbers with the exception of two uncatalogued specimens (2002-5-119, 2/20/04-27).

Table 3-3. Stable carbon and oxygen values for the taxa of the Gray Fossil Site, Tennessee.

Taxon	Na	$\delta^{13}\text{C}$ (‰)			$\delta^{18}\text{O}$ (‰)		
		Mean	SD	Range	Mean	SD	Range
<i>Tapirus polkensis</i>	23	-13.0	0.9	-14.1 to -10.9	-4.0	0.7	-5.2 to -2.3
<i>Teleoceras</i> cf. <i>T. hicksi</i>	4	-13.3	0.3	-13.6 to -13.0	-4.8	0.7	-5.5 to -3.9
Tayassuidae	3	-13.1	0.8	-14.0 to -12.4	-4.4	0.4	-4.9 to -4.1
cf. <i>Megatylopus</i> sp.	1	-13.8	-	-	-1.7	-	-
Gomphotheriidae	1b	-0.3	-	-	-4.2	-	-

a N = the number of different individuals sampled, the descriptive statistics do not include more than one tooth from an individual (no teeth were included that could have been missing teeth from an included individual).

b Gomphotherere tusk enamel was only available for isotope analysis.

Table 3-4. Serial carbon and oxygen isotope variation, per individual at the Gray Fossil Site, Tennessee.

Taxon	ETMNH #	Tooth	N	$\delta^{13}\text{C}$ (‰)			$\delta^{18}\text{O}$ (‰)		
				Min.	Max.	Range	Min.	Max.	Range
<i>Teleoceras</i> cf. <i>T. hicksi</i>	609	Lm3	12	-13.7	-13.0	0.7	-6.1	-5.0	1.1
<i>Teleoceras</i> cf. <i>T. hicksi</i>	781	LM1	14	-13.7	-12.7	1.0	-5.1	-3.8	1.2
<i>Tapirus polkensis</i>	595	Lm3	6	-11.9	-10.6	1.2	-4.0	-2.8	1.2
<i>Tapirus polkensis</i>	3424	RM3	8	-13.4	-12.3	1.2	-3.9	-2.8	1.1
Tayassuidae	779	Rm3	4	-13.2	-12.6	0.6	-5.6	-4.2	1.4
Gomphotheriidae	305	tusk	14	-0.7	0.2	1.0	-4.6	-4.0	0.6

Table 3-5. Carbon and oxygen isotope values for serial samples of ungulate enamel, Gray Fossil Site, Tennessee.

Sample	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
<i>Teleoceras</i> cf. <i>T. hicksi</i>	ETMNH 781	LM1
LGD-ETR1-S1	-13.3	-4.9
LGD-ETR1-S2	-13.4	-5.0
LGD-ETR1-S3	-13.7	-5.1
LGD-ETR1-S4	-13.4	-4.7
LGD-ETR1-S5	-13.2	-4.9
LGD-ETR1-S6	-12.8	-4.5
LGD-ETR1-S7	-13.1	-4.7
LGD-ETR1-S8	-13.2	-4.8
LGD-ETR1-S9	-13.3	-4.6
LGD-ETR1-S10	-13.2	-4.7
LGD-ETR1-S11	-13.3	-4.4
LGD-ETR1-S12	-13.4	-4.3
LGD-ETR1-S13	-13.2	-4.5
LGD-ETR1-S14	-12.7	-3.8
<i>Teleoceras</i> cf. <i>T. hicksi</i>	ETMNH 609	Lm3
LGD-ETR2-S1	-13.2	-5.7
LGD-ETR2-S2	-13.3	-5.1
LGD-ETR2-S3	-13.0	-5.0
LGD-ETR2-S4	-13.2	-5.2
LGD-ETR2-S5	-13.1	-5.0
LGD-ETR2-S6	-13.1	-5.3
LGD-ETR2-S7	-13.2	-5.3
LGD-ETR2-S8	-13.5	-5.7
LGD-ETR2-S9	-13.7	-6.1
LGD-ETR2-S10	-13.3	-5.9
LGD-ETR2-S11	-13.5	-5.9
LGD-ETR2-S12	-13.5	-5.8
<i>Tapirus polkensis</i>	ETMNH 3424	Lm3
LGD-ETT5-S1	-10.9	-4.0
LGD-ETT5-S2	-10.6	-3.6
LGD-ETT5-S3	-11.0	-2.8
LGD-ETT5-S4	-11.8	-3.1
LGD-ETT5-S5	-11.9	-3.1
LGD-ETT5-S6	-11.7	-2.8

Table 3-5 Continued.

<i>Tapirus polkensis</i>	ETMNH 608	RM3
LGD-ETT15-S1	-12.6	-3.0
LGD-ETT15-S2	-12.9	-3.0
LGD-ETT15-S3	-13.4	-3.7
LGD-ETT15-S4	-13.4	-3.9
LGD-ETT15-S5	-13.3	-3.3
LGD-ETT15-S6	-12.9	-2.9
LGD-ETT15-S7	-12.7	-2.9
LGD-ETT15-S8	-12.3	-2.8
Tayassuidae	ETMNH 779	Rm3
LGD-ETP1-S1	-12.6	-4.2
LGD-ETP1-S2	-13.2	-4.7
LGD-ETP1-S3	-12.8	-5.0
LGD-ETP1-S4	-12.8	-5.6
Gomphotheriidae	ETMNH 305	tusk
LGD-ETG1-S1	0.2	-4.2
LGD-ETG1-S2	-0.1	-4.2
LGD-ETG1-S3	-0.1	-4.1
LGD-ETG1-S4	-0.1	-4.2
LGD-ETG1-S5	-0.2	-4.0
LGD-ETG1-S6	-0.5	-4.1
LGD-ETG1-S7	-0.4	-4.2
LGD-ETG1-S8	-0.5	-4.1
LGD-ETG1-S9	-0.4	-4.2
LGD-ETG1-S10	-0.4	-4.4
LGD-ETG1-S11	-0.6	-4.4
LGD-ETG1-S12	-0.3	-4.5
LGD-ETG1-S13	-0.7	-4.4
LGD-ETG1-S14	-0.6	-4.6

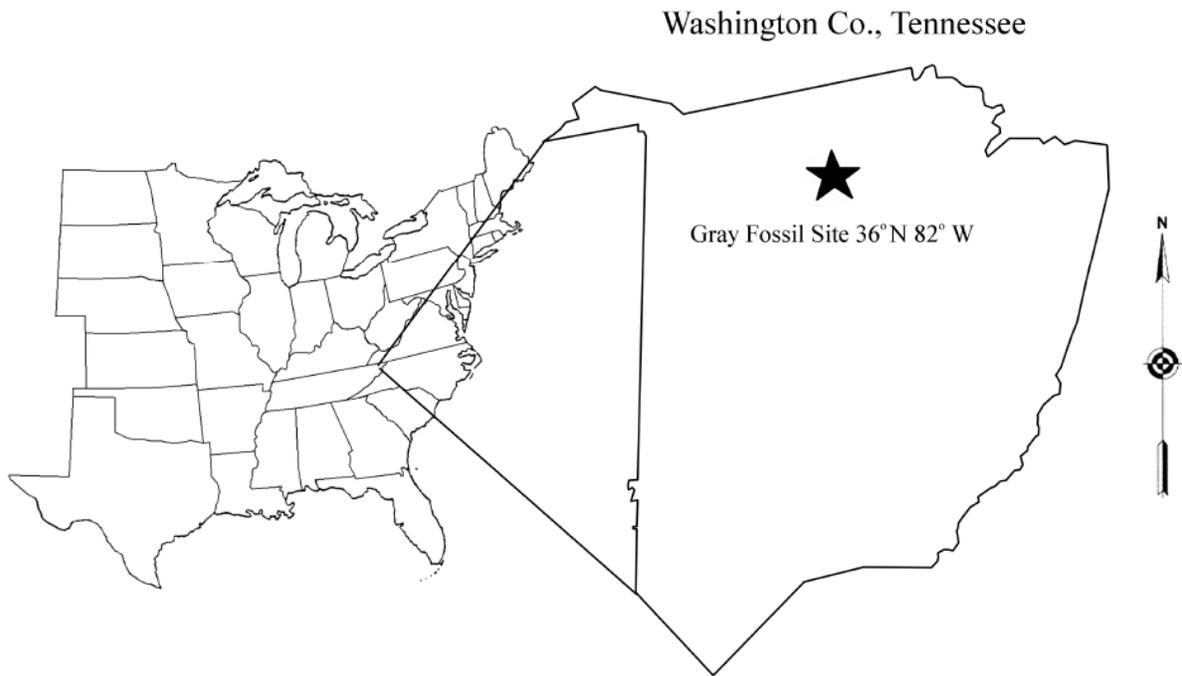


Figure 3-1. Location of the Gray Fossil Site, Tennessee, USA.

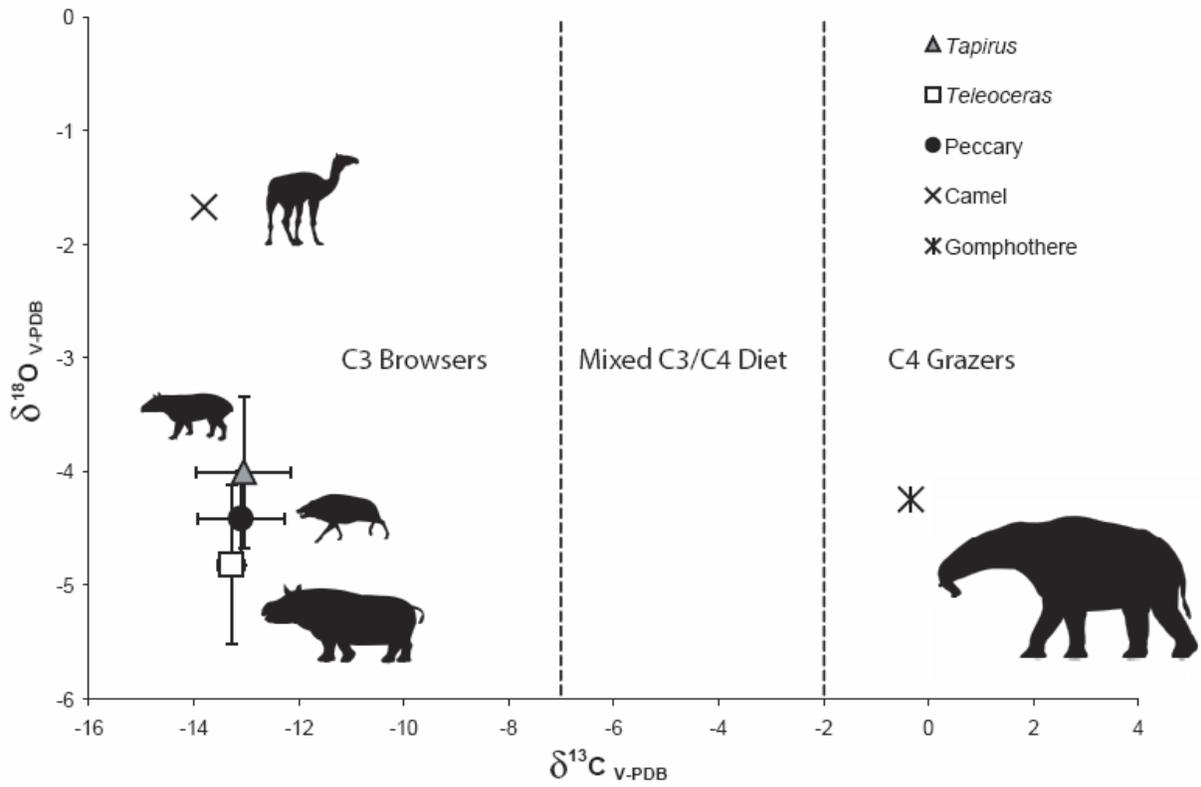


Figure 3-2. Stable carbon and oxygen isotope values from the ungulate taxa at the Gray Fossil Site. Symbols represent the mean value, while the error bars correspond to 1 standard deviation.

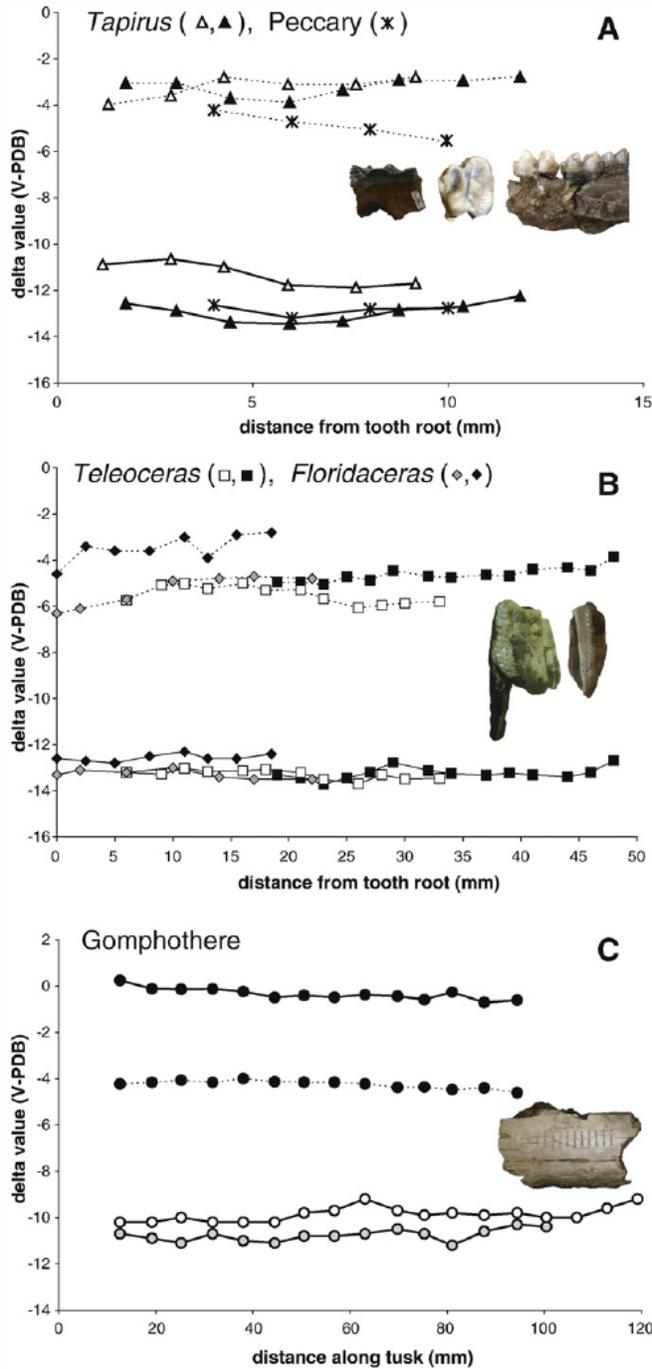


Figure 3-3. Serial samples of the ungulate taxa from the Gray Fossil Site, including: A) *Tapirus* (Δ, \blacktriangle), peccary (\times), B) *Teleoceras* (\blacksquare, \square), and C) the gomphotheres (\bullet). *Floridaceras* (\blacklozenge, \diamond) from the 15 Ma Gaillard Cut Local Fauna in Panama (MacFadden and Higgins, 2004) and late Miocene Gomphotheres (\bullet, \circ) from the Port of Entry Pit in Oklahoma, USA (Fox and Fisher, 2001), are included for comparisons in part B and C, respectively. Dashed lines represent oxygen values and solid lines indicate carbon values, while like colors correspond to the same individual per taxon.

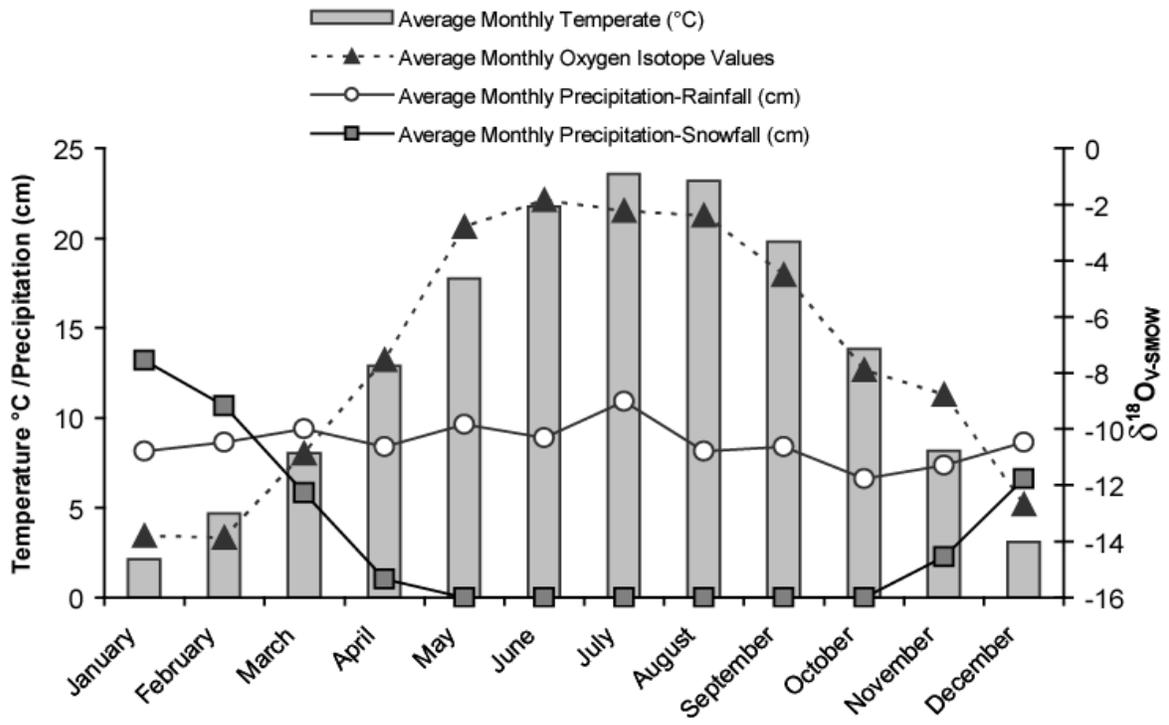


Figure 3-4. Average monthly temperate (°C), monthly oxygen isotope values, and monthly precipitation (rainfall, snowfall) in Johnson City/Bristol Tri-City Area, Tennessee. Oxygen isotope data are from Waterisotopes.org, temperature data are a 10-yr mean taken from station 401094/13877 and provided by the U.S. Department of Commerce and NOAA, www.ncdc.noaa.gov/oa/climate/climatedata.html. Remaining precipitation data (rainfall, snowfall) are from Climate Zone www.climate-zone.com.

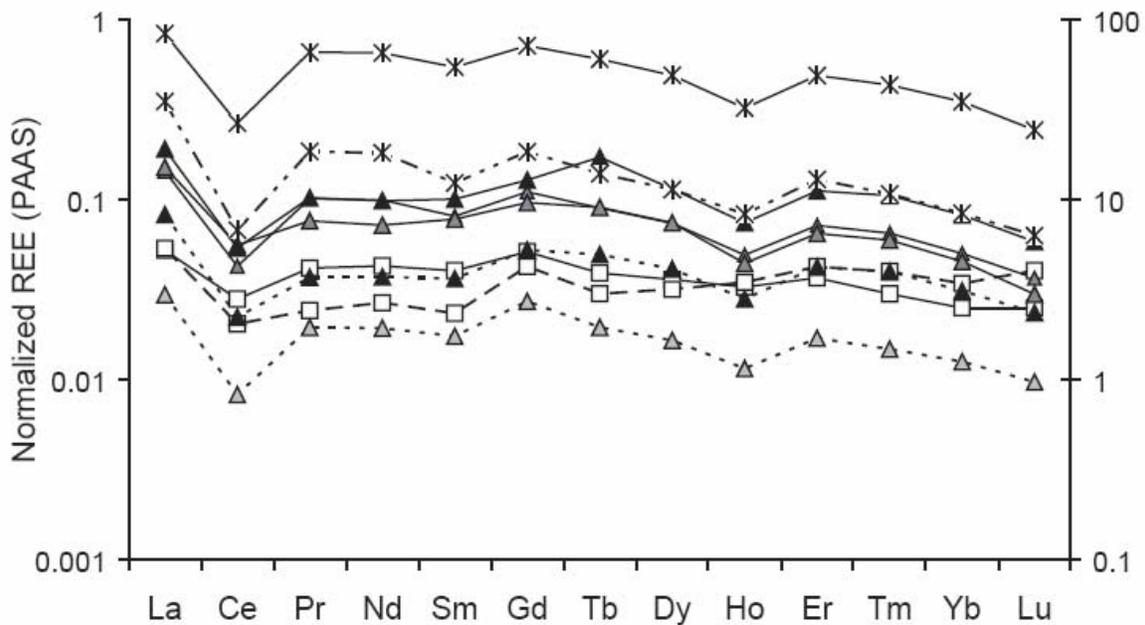


Figure 3-5. Normalized REE_(PAAS) concentrations of the (asterisk) gomphothere tusk, (triangles) *Tapirus*, and (square) *Teleoceras* teeth. Dentine and enamel REE concentrations are noted with dotted lines and solid black lines, respectively. Because gomphothere tusk enamel and dentin have higher absolute concentrations of REEs, they are plotted on the secondary y-axis (right).

CHAPTER 4
IDENTIFYING FOREST ENVIRONMENTS IN DEEP TIME USING FOSSIL TAPIRS:
EVIDENCE FROM EVOLUTIONARY MORPHOLOGY AND STABLE ISOTOPES

Introduction

Modern tapirs occupy densely-canopied forests throughout southern Mexico, Central America, South America, and southeast Asia (Salas, 1996; Brooks et al., 1997; Foerster and Vaughan, 2002; Tobler, 2002; Holden, 2003). Living tapirs are browsers and possess morphological features that are present in diverse clades of browsing mammals (e.g. low-crowned teeth, short mandibular diastema; MacFadden and Shockey, 1997; Mendoza et al., 2002). The masticatory morphology (morphological characters associated with the oral processing of food) of tapirs is interpreted to be highly conservative, retaining plesiomorphic characters through time (Colbert and Schoch, 1998). In addition to the conservative nature of morphological characters of browsers, tapiroids also appear to have browsed through time, as inferred from the stable carbon isotopes of their tooth enamel (MacFadden and Cerling, 1996; MacFadden and Shockey, 1997; Koch et al., 1998; Kohn et al., 2005; Feranec and MacFadden, 2006). Thus, if tapiroids are morphologically conservative and maintain stable carbon isotope values consistent with browsing, then their distributions can be used to identify forest environments in Deep Time.

The four extant tapirs, Baird's tapir (*Tapirus bairdii*), the lowland tapir (*Tapirus terrestris*), the mountain tapir (*Tapirus pinchaque*), and the Malayan tapir (*Tapirus indicus*) occupy forest environments, including: lowland forests, primary and secondary forests, Amazonian floodplains, and montane cloud forests (Brooks et al., 1997). Tobler (2002) also noted that tracks of *T. bairdii* were almost exclusively found in areas with dense vegetation and were rare in more open habitats. While *T. bairdii*, *T. terrestris*, and *T. indicus* inhabit forest environments (Salas, 1996; Brooks et al., 1997; Foerster and Vaughan, 2002; Tobler, 2002;

Holden, 2003), even the most ecologically divergent species, *T. pinchaque* (capable of occupying treeless paramo environments of greater than 3800 m elevation) lives in dense Andean forests more frequently than any other habitat type (Downer, 2001). Additionally, the Andean forests are necessary habitats for *T. pinchaque* as their canopies offer protection from predators and icy storms (Downer, 1996, 2001). Since living tapirs are consistently found either within, or in close proximity to, dense closed-canopy forests, they are model organisms for inferring forest environments of the past.

The diets of living tapirs generally consist of leaves, twigs, fiber, and fruit (Bodmer, 1991; Henry et al., 2000; Downer, 2001; Galetti et al., 2001; Tobler, 2002; Lizcano and Cavelier, 2004). Despite seasonal flooding, there is little variation in the diet of *T. terrestris* in Peru's Amazon floodplain (Bodmer, 1990). In contrast, *T. terrestris* in French Guiana consume fewer fruits and greater fiber seasonally, after peak fruiting (Henry et al., 2000). Even with potential seasonal variability in diet corresponding with fruiting events, living tapirs predominantly browse and forage for food throughout the year in forest environments (Bodmer, 1990; Salas, 1996; Tobler, 2002; Henry et al., 2000; Foerster and Vaughan, 2002).

Stable carbon isotope signatures of mammalian tooth enamel can be used to reconstruct the diet of extinct herbivores, including tapirs (DeNiro and Epstein, 1978; Quade et al., 1992; Cerling et al., 1997; MacFadden et al., 1999). Since the stable carbon isotope signatures of mammalian tooth enamel reflects the diet consumed (with a dietary enrichment rate, ϵ^* , of approximately 14.1‰ for medium to large bodied mammalian herbivores; Cerling and Harris, 1999), the diet of fossil tapirs can likewise be reconstructed through time. All previous studies of extinct mammals have demonstrated that within a given herbivore fauna, tapirs consistently have among the most negative $\delta^{13}\text{C}$ values (along with camelids; MacFadden and Cerling, 1996;

Koch et al., 1998; Kohn et al., 2005; Feranec and MacFadden, 2006). Based on modern analogues (e.g. Cerling et al., 2004), these values are interpreted to represent ancient forest habitats. In addition to their known ecological preference for forests, tapirs are model organisms for comparisons through Deep Time due to low intra-population variation of enamel stable carbon isotopic values (Grawe DeSantis, 2005). Given that a recent adult population of *T. bairdii* from Acapulco, Mexico was isotopically homogeneous in diet, with $\delta^{13}\text{C}$ variation of only 3‰, the carbon isotope values of adult fossil tapir specimens are likely to reflect those of a “fossil population” (Grawe DeSantis, 2005). Thus, comparisons of carbon isotope values of fossil tapirs through time will elucidate their dietary niche and proximity to forest environments.

Throughout the Cenozoic, North America underwent dramatic environmental transformations, as evident from anomalously warm tropical forests in high latitude North America during the Paleocene-Eocene Thermal Maximum (PETM) (Wing et al., 2005), dramatic declines in browsing taxa throughout the middle to late Miocene (Janis et al., 2000), and the expansion of C_4 grasslands during the late Miocene/early Pliocene (Wang et al., 1994; Cerling et al., 1997; Koch et al., 2004; Retallack, 2001; Stromberg, 2005). Because the expansion and contraction of forest environments are likely to affect the distributions of resident taxa, the presence of obligate forest dwellers can help reconstruct the distributions of their corresponding forest habitats in the past. Colbert and Schoch (1998) suggested that tapiroids have always resided in humid, mesothermal areas and that declining clade diversity during the Oligocene and Miocene reflects the contraction of these areas in comparison to Eocene distributions.

The primary objective of this study is to reconstruct the distribution of forest environments through time using fossil tapiroids as indicator taxa. While plant macrofossils and pollen are usually analyzed to understand ancient forest distributions, mammalian herbivores potentially

provide another line of evidence typically not available to paleobotanists. In order to use tapirs this way, I will first document their conservative morphology through time and compare them to the closely related horses (Equidae), a family with a considerably different evolutionary and adaptive history. Secondly, I will compare stable isotope values of tapirid tooth enamel through time to confirm their occupation as forest dwelling browsers. Lastly, I will use the Paleobiology Database (2006) to map tapiroid distributions through time, therefore, reconstructing forest distributions in Deep Time.

Materials and Methods

Morphology

Selected dental measurements were taken to quantify the evolution of crown height and body size proxies in relevant tapir specimens, ranging in age from early Eocene (Wasatchian, North American Land Mammal Age) to Recent. These measurements include: greatest anterior-posterior length of M1, m1, and m3; greatest transverse width of M1, m1, and m3; and greatest enamel crown height of M1, m1, and m3 (Mx, upper molar position; mx, lower molar position; Px, upper premolar position; px, lower premolar position). Relative ontogeny (based on tooth wear) was coded for each specimen as unworn, little wear, intermediate wear, and heavily worn. Individuals in the latter category were not used to calculate hypsodonty index (ratio of molar length to crown height).

Other measured characters that were taken, as available on individual specimens, include: greatest length of i1; greatest length of i3; length of mandibular diastema (i.e. from posterior to the canine to the anterior point of the p2); lower premolar row length (PRL); and lower molar row length (MRL).

Following Solounias and Moelleken (1993), MacFadden and Shockey (1997), and Mendoza et al. (2002), several cranial characters were coded to describe morphological evolution

related to browsing and grazing adaptations: glenoid fossa height above occlusal plane (low, high), paracondylar process length (short, long), anterior zygomatic arch (poorly or well developed), position of anterior most part of the orbit (dorsal to P3, P4, M1, M2, M3, or posterior to M3); shape of incisor arcade (curved, straight), and masseteric process above M1 (absent, present).

Specimens measured were from: the American Museum of Natural History (AMNH) Vertebrate Paleontology and Mammalogy collections in New York, New York, USA; the University of Florida/Florida Museum of Natural History (UF) Vertebrate Paleontology and Mammalogy collections in Gainesville, Florida, USA; and, the Yale Peabody Museum (YPM) Vertebrate Paleontology and Vertebrate Zoology collections in New Haven, Connecticut, USA. Data from the Paleobiology Database (2006) were also included, when available.

Stable Isotopes

Stable isotopic evidence was compiled from all available publications dealing with fossil tapirs from North America (MacFadden and Cerling, 1996; Koch et al., 1998; Kohn et al., 2005; Feranec and MacFadden, 2006). To this I have added previously unpublished data produced in our laboratory for specimens from the late Miocene McGehee and early Pliocene Palmetto Fauna localities in Florida and extant tapirs from Acapulco, Mexico.

All carbon isotope data are reported in the standard convention: $\delta^{13}\text{C}$ (per mil, ‰) = $[\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1] \times 1,000$, where R is the ratio of $^{13}\text{C}/^{12}\text{C}$ and the standard is VPDB (Pee Dee Belemnite, Vienna Convention; Coplen, 1994). All newly analyzed data were prepared using standard pre-treatment techniques (e.g. Koch et al., 1997; MacFadden and Higgins, 2004) and then analyzed on a VG Prism stable isotope ratio mass spectrometer with an in-line ISOCARB

automatic sampler in the Department of Geological Sciences at the University of Florida. The analytical precision based on replicate analyses is ± 0.1 ‰.

Inferred Forest Distributions

The locations and therefore known geographic distributions were plotted for all tapiroid taxa (Tapiroidea; classifications based on McKenna and Bell, 1997 and Colbert, 2005) compiled in the Paleobiology Database (2006). These data were used to produce the range maps for the Eocene through Recent. Present tapir distributions as determined from the International Union for Conservation of Nature and Natural Resources (IUCN) and the Species Survival Commission-Tapir Specialist Group's (SSC), "Tapir Status Survey and Conservation Action Plan" (Brooks et al. 1997), were added to the Present map.

Results and Discussion

Morphology

"For tapirs, all the evolutionary action was over after the Eocene¹." – Radinsky

The superfamily Tapiroidea has a fossil record extending back into the early Eocene, ~55 million years ago (McKenna and Bell, 1997; Colbert, 2005; Paleobiology Database, 2006; Figure 4-1). Here we present both qualitative and quantitative morphological results demonstrating the conservative nature of fossil tapirs as compared to a more rapidly evolving clade within the Perissodactyla, i.e. the classic example of fossil horses (family Equidae; e.g, Simpson, 1953; MacFadden, 1992). As I assert above, the bradytelic (i.e. very slow, *sensu* Simpson, 1953) evolution in Cenozoic tapirs allows ecological interpretations relative to modern *Tapirus* far back into the fossil record.

¹ Paraphrased comment, L. Radinsky to B. MacFadden, mid 1970s

Several previous studies have demonstrated that there are suites of qualitative morphological characters of the cranium and mandible in mammalian herbivores that represent adaptations for either browsing or grazing (Solounias and Moelleken, 1993; MacFadden and Shockey, 1997; Mendoza et al., 2002; Table 4-1). Based on the distribution of these characters in the fossil record, it is known that browsing adaptations are primitive (plesiomorphic), whereas grazing characters are derived (apomorphic). These morphologies are illustrated (Figure 4-2) in four representative examples, the Oligocene tapiroid *Protapirus* and modern *Tapirus* as compared to the Oligocene equid *Mesohippus* and modern *Equus*. As can be seen in both table 4-1 and Figure 4-2, primitive morphologies of the cranium and mandible are demonstrated in *Protapirus*, *Mesohippus*, and *Tapirus*, whereas derived morphologies are demonstrated in *Equus*. This indicates that the adaptive morphology of *Tapirus* has evolved little since the early Cenozoic when both the Tapiroidea and Equidae had browsing adaptations (Table 4-1, Figure 4-2). While the Equidae subsequently underwent explosive evolution in cranial and mandibular morphology, particularly since the Miocene (Simpson, 1953; Radinsky, 1984; MacFadden, 1992), tapirs demonstrate bradytelic (slow) evolution. The comparative evolution and analysis of multiple characters that are associated with dietary strategies strengthens our dietary interpretations through time.

Most of the evolution described above results from major morphological changes to the masticatory complex, including the great expansion of cheek tooth crown heights observed in advanced horses (Simpson, 1953; Radinsky, 1984; MacFadden, 1992). Given the relatively common occurrence of fossil horse teeth, as opposed to the rarely preserved cranial and mandibular morphology, equid dentitions are frequently cited as prime examples of macroevolution. One such dental character, hypsodonty index (HI), is an informative means of

comparing the evolutionary morphology in clades of mammalian herbivores. Previous studies have shown that extinct mammal species with HIs < 1 are primarily browsers and those with HIs > 1 , although classically interpreted as primarily grazers (e.g. Simpson, 1953; MacFadden, 1992), actually have the evolutionary capacity to be either browsers or grazers (MacFadden et al., 1999; Feranec, 2003; MacFadden, 2005). Horses were primitively short-crowned, with HIs all < 1 until about 20 million years ago. Thereafter, several clades of horses underwent explosive, rapid evolution of crown heights, resulting in HIs ranging from > 1 to 3 (Figure 4-3; although one equid clade, the browsing anchitheres, retained the primitive morphology). The explanation for this rapid increase in HIs during the Miocene is initially to exploit a new food resource, grasses, which were spreading over many continental landscapes. This “Great Transformation” (Simpson, 1953; Stromberg, 2005) fundamentally affected both the morphological and ecological evolution of the Equidae. In contrast to the Equidae, a very different pattern is seen in the evolution of HIs in Tapiroidea (Figure 4-3). All tapiroid taxa measured for this study ranging in age from ~ 53 Ma to the present have HIs < 0.7 . Thus, while horses were rapidly evolving in response to the changing environments, the bradytelic (slowly evolving) tapirs are characterized by stasis in crown heights.

Body size is a fundamentally important character in understanding ecological adaptations of individual species (e.g. Eisenberg, 1981). Although body size is difficult to estimate in extinct species, molar dimensions can serve as a proxy for relative body size (e.g. MacFadden, 1986; Damuth and MacFadden, 1990). In this paper, I use m1 length as a relative indicator of tapir body size. With the exception of the three modern species *T. terrestris*, *T. bairdii*, and *T. pinchaque* and the fossil taxon *Tapirus polkensis* that have declined in m1 length since the late Miocene, the m1 length within other species within the Tapiroidea has increased in size by about

2.5 times in approximately 50 million years (Figure 4-4). This increase in m1 length, and corresponding inferred body size increase, appears to be linear and relatively gradual, interpreted to represent relative stasis, both in morphology and diet. This is in contrast to the explosive pulse of evolution seen in fossil horses during the Neogene after about 20 million years ago (MacFadden, 1986). As will be seen below, the conservative morphology and browsing diet demonstrated here for fossil tapirs are also corroborated by evidence from stable isotopes.

Stable Carbon Isotopes

As opposed to the traditional method of interpreting extinct mammalian herbivores as grazers or browsers using morphological characters, stable carbon isotope ratios can be used to interpret ancient diets (Cerling et al., 1993, 1997; Wang et al., 1994; MacFadden and Shockey, 1997; MacFadden et al., 1999; Zazzo et al., 2000). Stable carbon isotope analysis of fossil tooth enamel provides dietary information about the respective taxon, because carbon is incorporated into the lattice of enamel hydroxylapatite retaining an isotopic signal that is reflective of plants consumed (Krueger, 1991; Lee-Thorp and van der Merwe, 1991; Cerling et al., 1997; Cerling and Harris, 1999). Because $^{13}\text{C}/^{12}\text{C}$ ratios in plants vary depending on plant photosynthetic pathways and stable carbon isotopes do not decay with time (Ehleringer and Monson, 1993) in the absence of diagenesis (postmortem chemical alteration), we can look at ^{13}C and ^{12}C ratios of the past similarly to ratios of ^{13}C and ^{12}C today (Cerling et al., 1997). The $\delta^{13}\text{C}$ values of medium to large-bodied ungulates are enriched by approximately 14.1‰ (although non-ruminants, such as tapirs, may be enriched by 12-13‰), as compared to plants consumed (Cerling and Harris, 1999). Therefore, enamel $\delta^{13}\text{C}$ values $\leq -9\text{‰}$ (possibly as enriched as -7‰ due to modern atmospheric CO_2 enrichment; Cerling et al., 1997; Passey et al., 2002) reflect a pure C_3 diet and $\delta^{13}\text{C}$ values $\geq -2\text{‰}$ indicate a predominantly C_4 diet (MacFadden et al., 1996; Cerling et al., 1997, 1999, 2004; Cerling and Harris, 1999).

Stable carbon isotopes of extinct/extant taxa can also be used to reconstruct forest canopy density due to greater ^{13}C discrimination occurring in dense closed canopies as compared to less dense/open C_3 environments (van der Merwe and Medina, 1989; Cerling et al., 2004). Since $\delta^{13}\text{C}$ values increase with decreasing canopy density and/or increasing distance from dense forest edges (van der Merwe and Medina, 1989; Kapos et al., 1993; West et al., 2001), more depleted $\delta^{13}\text{C}$ values of mammalian herbivores reflect the consumption of browse in denser canopied forests (van der Merwe and Medina, 1991; Cerling et al., 2004). By examining the stable isotopes of fossil tapirs and other extinct mammalian herbivores, we can document dietary changes through time.

Stable carbon isotopes of fossil tapir enamel have been analyzed from several North American sites spanning the past ~10 million years (MacFadden and Cerling, 1996; Koch et al., 1998; Kohn et al., 2005; Feranec and MacFadden, 2006; Figure 4-5). The localities included in this analysis are, from oldest to youngest (Ma): Love Bone Bed (~9.5); McGehee and Mixons (~7.5); Withlacoochee (~7); Palmetto (~4.5); Haile 15A, Macasphalt, Port Charlotte, Punta Gorda and Santa Fe 1 (~2.5); Leisey 1A (~1.5); Harleyville (~0.4); Cutler, Hornsby Springs, Ichetucknee, Page-Ladson, Rock Springs, and Santa Fe (~0.1-0.01) (MacFadden and Cerling, 1996; Koch et al., 1998; Kohn et al., 2005; Feranec and MacFadden, 2006; Figure 4-5). Fossil tapirs consistently demonstrate diets composed of predominantly C_3 vegetation, with enamel $\delta^{13}\text{C}$ values ranging from -10.1 to -14.3‰ (Figure 4-5). Additionally, fossil tapirs likely maintain their presence in denser canopied forests because their $\delta^{13}\text{C}$ values consistently are among the most ^{13}C depleted isotopic values as compared to other co-occurring mammalian herbivores (Figure 4-5). For example, fossil horses from these sites demonstrate a pattern different from tapirs, instead consuming more isotopically enriched vegetation (Figure 4-5).

Since their first appearance approximately 2.5-1.5 Ma during the Great American Biotic Interchange (Stehli and Webb, 1985), fossil and extant South American tapirs inhabit dense canopied environments, as inferred from stable isotopes (MacFadden and Shockey, 1997; Grawe DeSantis, 2005). MacFadden and Shockey (1997) interpreted *Tapirus tarijensis* as a browser (based on morphological characters), along with peccaries (*Tayassu* sp.), deer (*Hippocamelus* sp.), and llamas (*Palaeolama weddelli*) at the Tarija Pleistocene (0.5 to 1.0 Ma) site in Bolivia. As is also seen in ancient North American ecosystems, the isotopic values of *T. tarijensis* of -13.4 to -10.5‰ are among the most ¹³C depleted of all herbivores sampled within the Tarija fauna (total whole faunal range of -13.4 to -3.4‰; MacFadden and Shockey, 1997). Similarly, the modern tapir *Tapirus bairdii* (from specimens collected between 1873-74 in Acapulco, Mexico) demonstrates mean $\delta^{13}\text{C}$ values of -14.6‰ (Grawe DeSantis, 2005), consistent with their classification as forest occupying browsers. Because tapirs consume fruits that have isotopic values more enriched than corresponding sub-canopy foliage (due to vertical stratification of $\delta^{13}\text{C}$ values; van der Merwe and Medina, 1989; Cerling et al., 2004) their dietary $\delta^{13}\text{C}$ values are likely more enriched than the foliage in these environments. Therefore, tapirs likely reside in even more densely forested environments than indicated isotopically. In conjunction with their conservative morphology, the depleted $\delta^{13}\text{C}$ values justify tapirs as robust indicators of forest environments in Deep Time.

Distributions

From the Paleocene-Eocene Thermal Maximum to the Miocene-Pliocene expansion of C₄ grasslands, North America underwent great environmental change throughout the Cenozoic. Paleobotanical studies document dramatic vegetation shifts in mesothermal (i.e. moderate moisture and heat with mean temperatures between 15-20° C, *sensu* Wolf, 1975 modified from de Candolle, 1874) broad-leaved evergreen forests, contracting from Eocene distributions of 60°

latitude from the equator, to only 35° during the sharp cooling of the early Oligocene (Potts and Behrensmeyer, 1992; Wing, 1998). Megathermal (i.e. humid and warm with mean temperatures $\geq 20^\circ\text{C}$, *sensu* de Candolle, 1874) vegetation also became restricted to within 15° from the equator during the Oligocene, compared to early Eocene latitudinal distributions of 60-65° and modern ranges of 20-25° (Potts and Behrensmeyer, 1992). Corresponding to these shifts in vegetation, cooling occurred from the late Eocene to early Miocene, with periodic warming events that consistently declined in temperature from preceding warming events (Wolfe, 1994). While these changes in forest distributions are inferred from paleobotanical evidence including pollen, plant macrofossils, and subsequent Climate-Leaf Analysis Multivariate Program (CLAMP) analyses, tapirs can provide an independent line of evidence for the presence of ancient forests in Deep Time. As Colbert and Schoch (1998) suggested, the lack of significant tapiroid remains in the Oligocene and Miocene may be a result of declines in the mesothermal forests they likely inhabited.

The Paleobiology Database (2006) is a valuable tool for analyzing the distribution of ancient faunas both temporally and spatially. Using the Paleobiology Database (2006), I generated maps of tapiroid distributions in North and Central America from the Eocene to the present (Table 4-2, Figure 4-6). During the Eocene, tapiroid distributions are most wide-ranging, extending from central Mexico to Arctic Canada (Table 4-2, Figure 4-6). The widespread distribution of Tapiroidea during the Eocene correlates with paleobotanical evidence that suggests extensive mesothermal and megathermal vegetation ranges with boreotropical flora extending to at least 65° N in North America (Wolf, 1975; Wing and Sues, 1992; Wing, 1998). However, based on the presence of tapiroids at latitudes up to 78.5° N during the Eocene, boreotropical flora may have extended farther north than previously anticipated. This is in

agreement with the presence of semi-tropical fossil forests found at Axil Heiberg Island of ~80° N latitude (Christie and McMillan, 1991). Additionally, the dramatic decline in tapiroid latitudinal ranges during the Oligocene (Table 4-2, Figure 4-6) is likely a result of sharp global cooling that decreased their mesothermal habitats (Colbert and Schoch, 1998; Wing, 1998). After the Oligocene, tapiroid ranges expand through the Pleistocene (Table 4-2, Figure 4-6) concurrently with fluctuating warming and cooling events (including the Miocene Thermal Maximum at ~16 Ma; Wing, 1998). These tapiroid range expansions occur from northern to southern regions with relatively consistent upper latitudinal range limits of between 40-46° N, from the Miocene to the Pleistocene (Table 4-2, Figure 4-6). Subsequently, the upper range limits of *Tapirus* contracted from 40° to 21° N during the last ~2 million years (Table 4-2, Figure 4-6). This recent contraction likely resulted from the inability of *Tapirus* to live in the seasonally cool and/or glacially inundated higher latitudes. Overall, tapiroid distributions correlate well with paleobotanically derived climatic inferences. Along with tapiroid morphology and isotopic data, these distribution maps provide reconstructions of ancient forest environments with both temporal and spatial resolution.

Conclusions

Cenozoic tapirs have been under appreciated, mostly because as Len Radinsky noted in the 1970's, the most interesting phases of their evolution occurred during the Eocene. Thereafter, despite significant global change in terrestrial ecosystems, tapirs are prime examples of Simpson's (1953) concept of bradytely, i.e. a group demonstrating slow, or arrested evolution. This mostly resulted from Tapiroids being well adapted to their respective adaptive zone (niche complex in modern parlance) in ancient forests. Tapirs may not be a good group to investigate evolution "in the fast lane," but they are model taxa for paleoecological reconstructions. The morphologic, isotopic, and biogeographic analyses presented above indicate that tapiroids are

excellent indicators of ancient forest environments, and adds to our knowledge of these ancient habitat types based on other fossil evidence, e.g. as derived from paleobotany. As additional localities are discovered and analyzed in the future, we are bound to find more evidence of herbivore-plant interactions such as those exemplified by extinct forest-dwelling tapirs.

Table 4-1. Comparison of craniodental features between the Oligocene tapiroid *Protapirus*, modern *Tapirus*, the Oligocene equid *Mesohippus*, and modern *Equus*.

Craniodental feature	<i>Protapirus Tapirus</i>		<i>Mesohippus</i>	<i>Equus</i>
	(Oligocene)	(Modern)	(Oligocene)	(Modern)
Hypsodonty Index	< 1	< 1	< 1	> 1
Relative size of incisors	i1 > i3	i1 > i3	i1 > i3	i1 ≈ i3
Shape of Incisor arcade	curved	curved	curved	straight
Relative length of premolar tooth row	PRL < MRL	PRL < MRL	PRL < MRL	PRL > MRL
Length of mandibular diastema	short <2 x m1 length	short <2 x m1 length	short <2 x m1 length	long >2 x m1 length
Masseteric prominence above M1	absent	absent	absent	present
Position of the orbit	above or anterior to M2	above or anterior to M2	above or anterior to M2	posterior to M3
Anterior extension of the zygomatic arch	poorly developed	poorly developed	poorly developed	well developed
Height of the glenoid fossa above the occlusal plane	low	low	low	high

The craniodental features were modified from those compiled by Mendoza et al. (2002). PRL=premolar row length, and MRL=molar row length.

Table 4-2. Summary of Paleobiology Database (2006) results of tapiroid localities in North and Central America. Additionally, Holocene collections include present localities taken from the IUCN Tapir Status Survey and Conservation Action Plan (Brooks et al., 1997).

Geological Epoch	Age Range (million years ago)	Latitudinal Range	Total Latitudinal Range
Eocene	54.8-33.7	21° N to 79° N	58
Oligocene	33.7-23.8	42° N to 50° N	8
Miocene	23.8-5.3	28° N to 46° N	18
Pliocene	5.3-1.8	20° N to 42° N	22
Pleistocene	1.8-0.01	9° N to 40° N	31
Holocene	0.01-present	9° N to 21° N	12

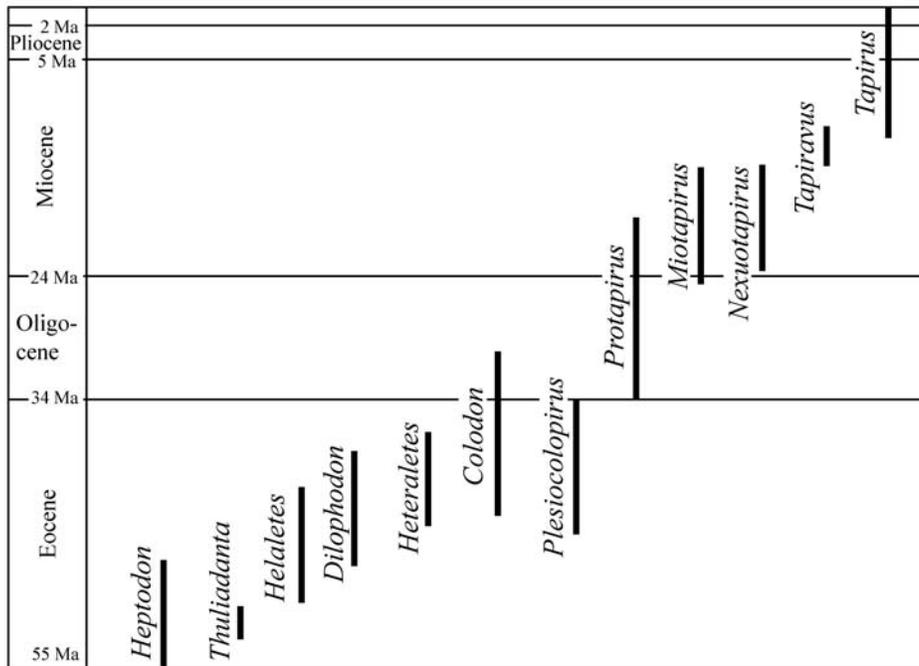


Figure 4-1. Temporal distributions of the tapiroid genera analyzed in this study. The ranges are taken from the Paleobiology Database (2006). Following McKenna and Bell (1997) and Colbert (2005), *Heptodon* is included in the Tapiroidea.

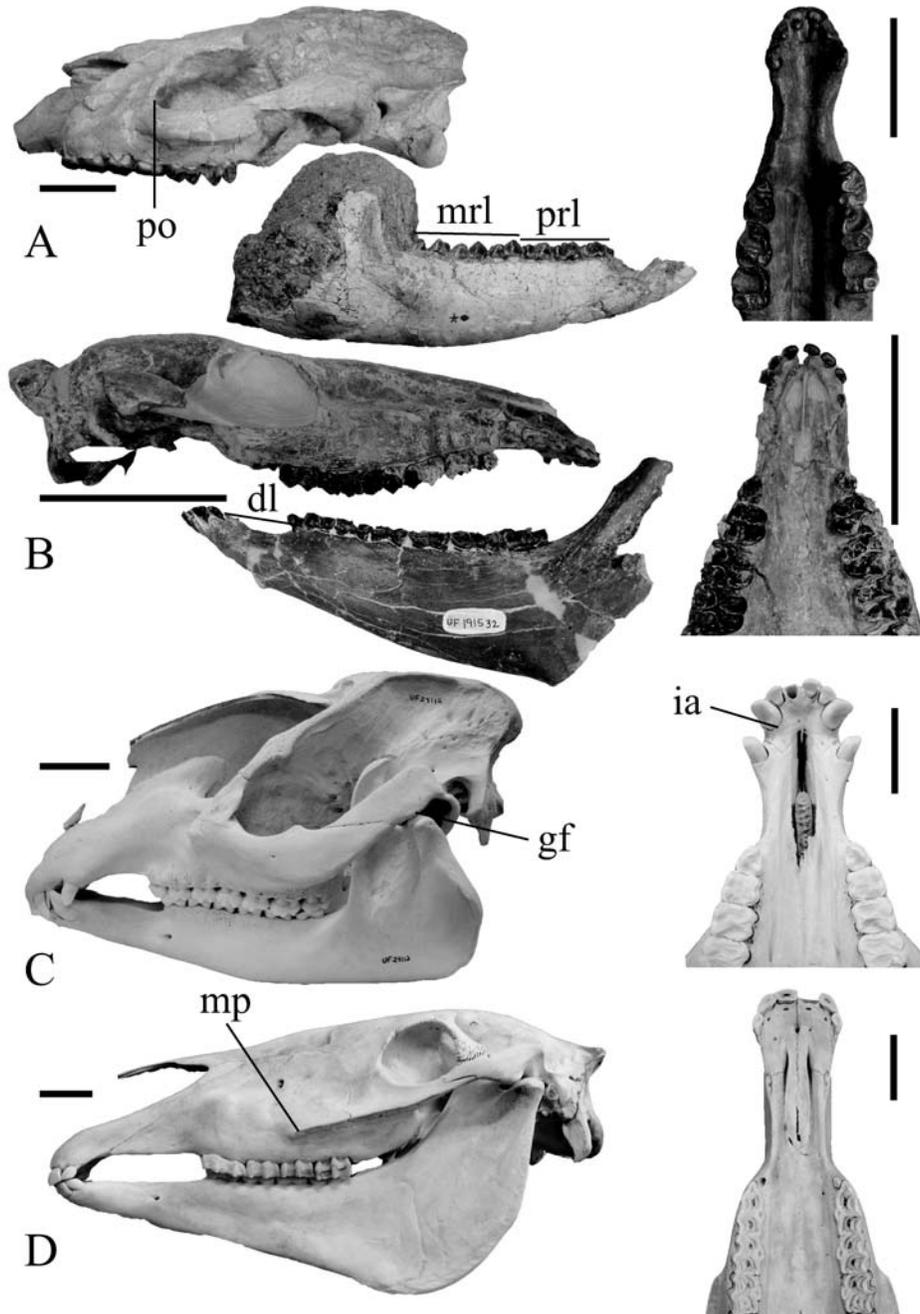


Figure 4-2. Fossil specimens of the (A) tapirid *Protapirus* (left: YPM 11165; right: AMNH 661) from the middle Oligocene (“Protoceras beds”), South Dakota, and (B) equid *Mesohippus* (cranium, UF 201941, and UF191532, mandible) from the late Eocene/early Oligocene White River Group, western Nebraska. Modern (C) tapir (*Tapirus*; UF 24112) and (D) horse (*Equus*; UF225366) specimens are from the UF/FLMNH collection. Abbreviations are, as follows: dl=diastema length; gf=glenoid fossa; ia=incisor arcade; mrl=molar row length; mp=masseteric prominence; po=position of orbit; and, prl=premolar row length. All scale bars equal 5 cm.

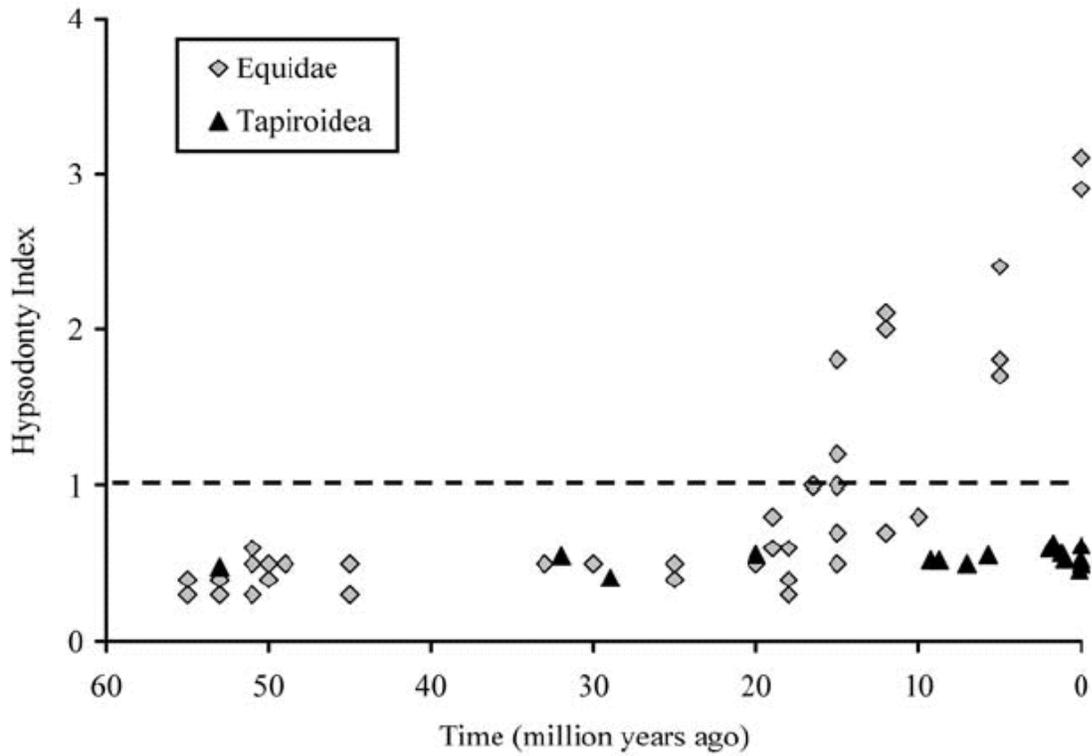


Figure 4-3. Hypsodonty index of two contrasting clades of perissodactyls, i.e. Equidae and Tapiroidea, throughout the past 55 million years. Data for Equidae are taken from MacFadden (1992; Figure 11.6). Tapiroid values were measured from collections at the AMNH, YPM, and FLMNH. Mean values of the following taxa are included: *Colodon* (including *C. occidentalis*), *Heptodon*, *Miotapirus*, *Protapirus* (including *P. simplex*), *Tapiravus* (including *T. validus*), and *Tapirus* (including *T. bairdii*, *T. haysii*, *T. indicus*, *T. johnsoni*, *T. pinchaque*, *T. simpsoni*, *T. terrestris*, *T. veroensis*).

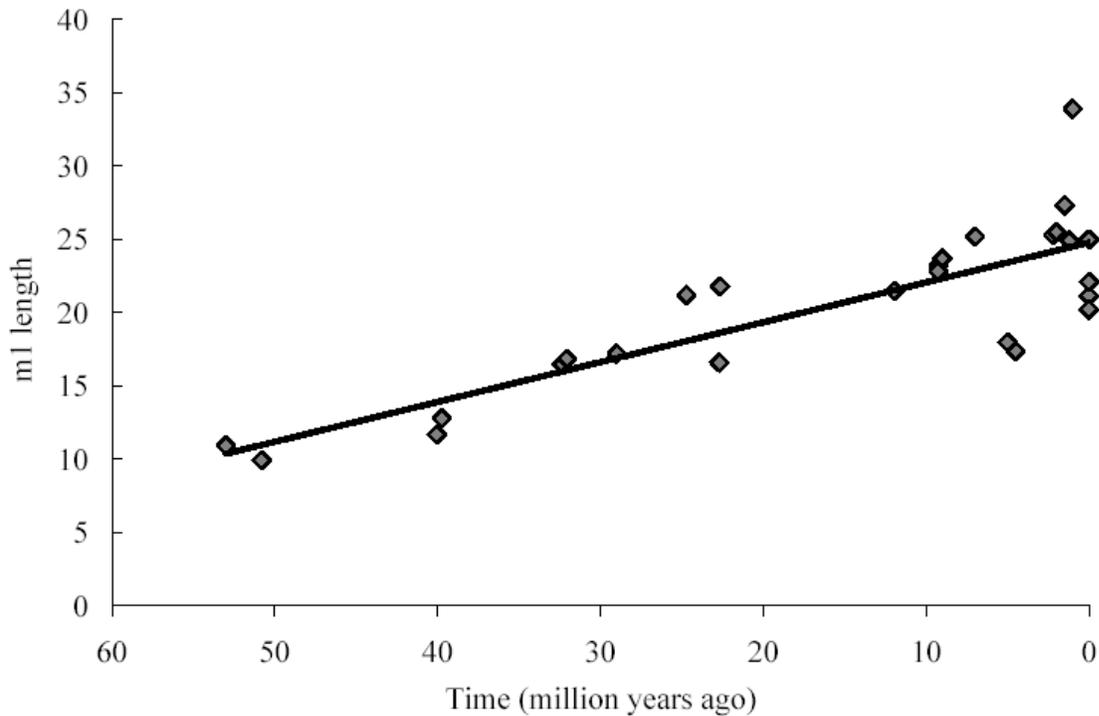


Figure 4-4. North American fossil tapiroid and extant Central American and South American tapir m1 lengths through time as a proxy for body size evolution. The linear regression of all data analyzed, $R^2=0.73$. If you exclude the three extant tapirs (*T. bairdii*, *T. pinchaque*, and *T. terrestris*) and the fossil *Tapirus polkensis*, which demonstrate recent declines in body size since the late Miocene, $R^2=0.94$. Data were measured from specimens at the AMNH, YPM, FLMNH, and compiled from the Paleobiology Database (<http://paleodb.org>). The following taxa were included: *Colodon* (including *C. occidentalis*), *Helaletes*, *Heptodon*, *Miotapirus*, *Nexuotapirus* (including *N. marslandensis*, *N. robustus*), *Plesiocolopirus* (including *P. hancocki*), *Protapirus* (including *P. obliquidens*, *P. simplex*), *Tapiravus* (including *T. validus*), and *Tapirus* (including *T. bairdii*, *T. haysii*, *T. indicus*, *T. johnsoni*, *T. pinchaque*, *T. simpsoni*, *T. terrestris*, *T. veroensis*).

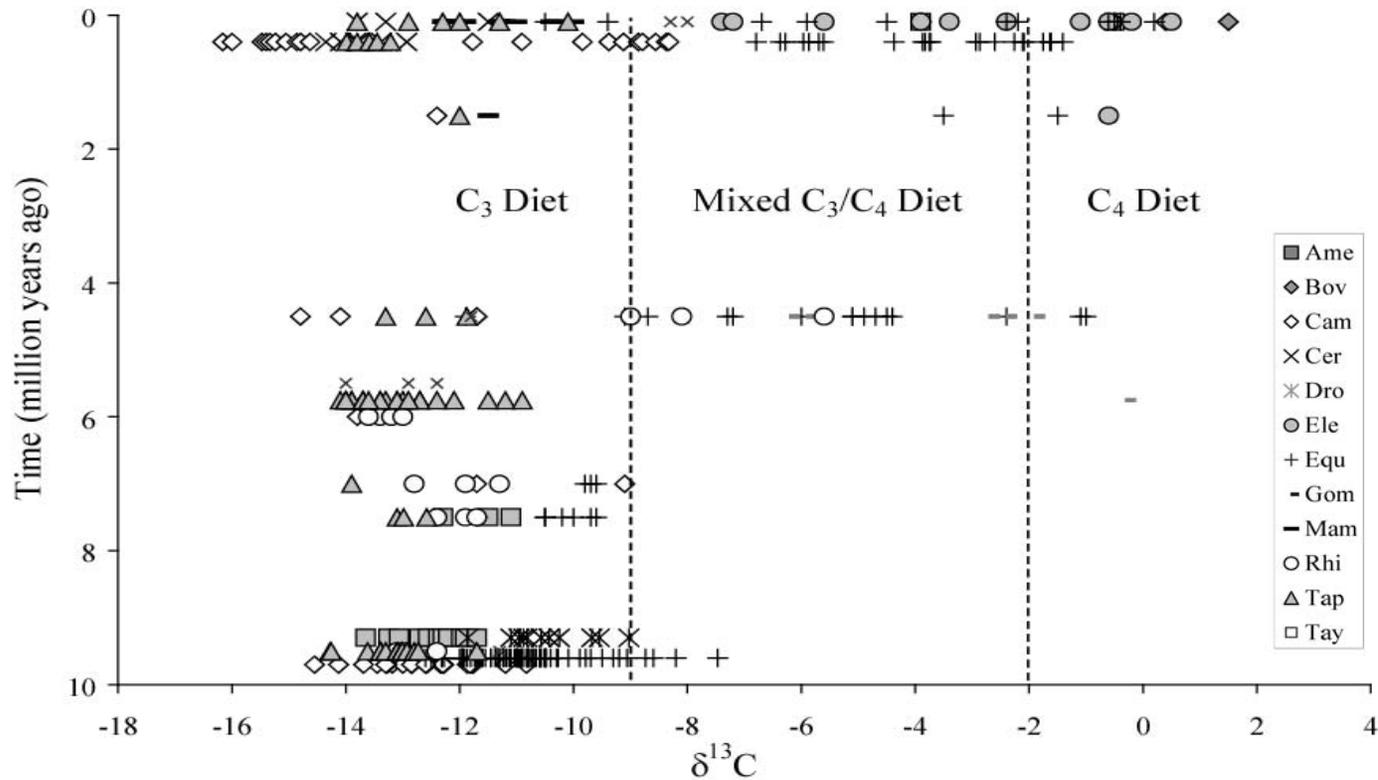


Figure 4-5. Carbon isotope data for tooth enamel of fossil tapirs and their associated faunas for the past 10 million years in North America (compiled from MacFadden and Cerling, 1996; Koch et al., 1998; Kohn et al., 2005; Feranec and MacFadden, 2006). Additional new isotopic data sampled from the McGehee and the Palmetto Fauna localities in Florida are also included. Family abbreviations are, as follows (number of samples noted in parentheses): Ame=Amebelodontidae (N=12), Bov=Bovidae (N=3), Cam=Camelidae (N=51), Cer=Cervidae (N=9), Dro=Dromomerycidae (N=11), Ele=Elephantidae (N=11), Equ=Equidae (N=141), Gom=Gomphotheriidae (N=5), Mam=Mammutidae (N=14), Rhi=Rhinocerotidae (N=12), Tap=Tapiridae (N=33), and Tay=Tayassuidae (N=4). Each data point represents a single specimen. Additionally, all data points between 9-10 Ma are from the Love Bone Bed Local Fauna ~9.5 Ma; however, they are slightly offset to improve visual clarity.

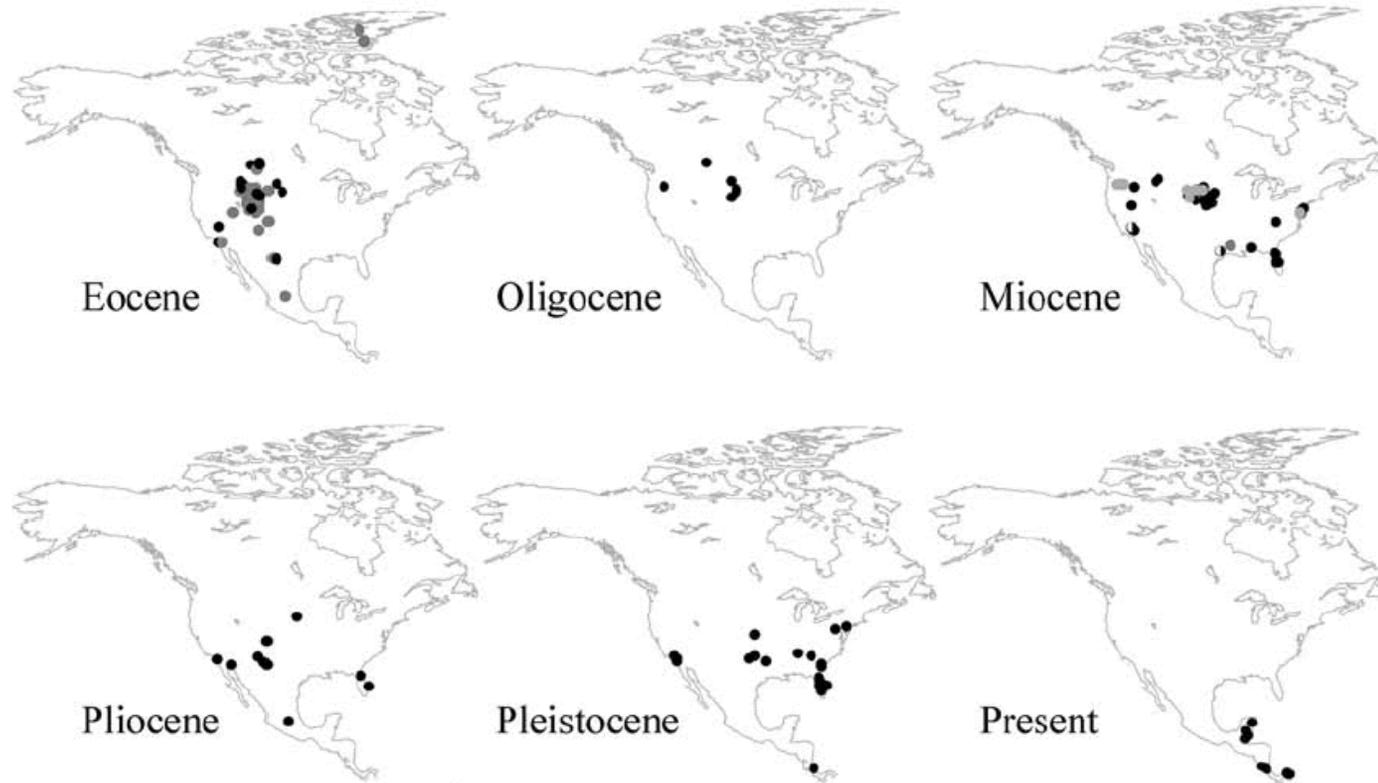


Figure 4-6. Maps of tapiroid localities on continental North America from the Eocene through the present. The maps were created from the Paleobiology Database (<http://paleodb.org>). For the Eocene, gray circles (●) indicate early Eocene (Wasatchian, Bridgerian; ~55-46 Ma) localities and black circles (●) represent late Eocene (Uintan, Chadronian; ~46-34 Ma) sites. The Miocene is also sub-divided, with gray circles (●) signifying early Miocene (late Arikarean, Hemingfordian, Barstovian; ~24-11 Ma) ages, black circles (●) representing the late Miocene (Clarendonian, Hemphillian; ~11-5 Ma), and black and white circles (◐) indicating undifferentiated Miocene localities. Additionally, present tapir distributions as summarized from the IUCN Tapir Status Survey and Conservation Action Plan (Brooks et al., 1997) were added to the present maps.

CHAPTER 5 CONCLUSION

Understanding the ecology of modern and ancient forests is critical to comprehending the context of mammalian evolution. Collectively, the chapters presented in this dissertation clarify the paleoecological dynamics of forest environments and their mammalian inhabitants throughout the Cenozoic. Through a detailed examination of the stable isotope ecology of modern tapirs, I clarified the paleoecology and paleoclimatology of ancient tapir environments in the Appalachians and throughout the New World. Specifically, I document dietary variation in extant tapirs and further clarify relationships between stable carbon and oxygen isotopes and climatic and geographic variables (Chapter 2). Next (Chapter 3), I elucidate the paleoecology and paleoclimatology of a potential Neogene Appalachian forest refuge. Subsequently (Chapter 4), I document the conservative dietary niches of extant tapirs and their ancestors and uses tapirs as model organisms to document forest distributions throughout the Cenozoic in the New World.

In Chapter 2, stable carbon and oxygen isotopes of extant tapirs are quantified to test hypotheses regarding ontogenetic dietary shifts, stable isotope variation at the population level, and relationships between stable isotopes and climatic variables. A population of extant tapirs (*Tapirus bairdii*) from Acapulco, Mexico demonstrates that $\delta^{13}\text{C}$ values of late erupting teeth are significantly greater than the early erupting first molar, indicating that juveniles are consuming ^{13}C deplete milk and/or browsing in the denser canopy. The $\delta^{18}\text{O}$ values of late erupting teeth (P4, M3) are significantly different from each other, likely reflecting seasonal differences due to their chronological eruption. Dietary variation at the population level is low with $\delta^{13}\text{C}$ variation of ~2-3‰ for individual tooth positions. Additionally, extant tapir (*T. bairdii*, *T. pinchaque*, *T. terrestris*) $\delta^{18}\text{O}$ values are constrained by climatic and geographic variables. Most notably, $\delta^{18}\text{O}$ values of *T. bairdii* decrease with decreasing precipitation frequency (mean number of

precipitation days per month). *T. terrestris* is typically present in areas with greater precipitation than *T. bairdii* and $\delta^{18}\text{O}$ values are instead significantly correlated with $\delta^{13}\text{C}$ values. These data indicate that tapirs in wetter areas derive a larger proportion of their water from leaves experiencing less evaporation in denser canopies, while *T. bairdii* is interpreted to increase water consumption by drinking when present in drier areas. An understanding of extant tapir stable isotope ecology improves and validates ecological interpretations of these elusive mammals both today and in the past. Additionally, these data help constrain the paleoecological and paleoclimatic hypotheses tested in Chapters 3 and 4.

In Chapter 3, I clarified the paleoecology of mammalian herbivores and their floral environments during the Neogene in the poorly understood Appalachians, which is characterized by a paucity of relevant fossil localities during this time period. Global climate change and the expansion of C_4 grasslands were interpreted to have taken place concurrently (Cerling et al., 1993, 1997; Wang et al., 1994); however, the Gray site's flora and fauna suggest a forest refugium (Wallace and Wang, 2004). Therefore, stable isotope analyses of bulk and serial samples of fossil tooth enamel from all ungulates present at the Gray site were used to elucidate the ancient ecology of resident fauna. All of the ungulate taxa (tapirs, rhinos, camels, and peccaries), with the exception of the gomphothere, yield mean stable carbon isotope tooth enamel values suggestive of forest-dwelling browsers in a moderately dense forest. The lack of significant C_4 plant consumption suggests the presence of forests large enough to independently support the continued browsing of sustainable populations of browsers from the Gray site. In contrast, bulk and serial carbon isotopes from the gomphothere tusk support a diet consisting of C_4 grasses, suggesting the presence of C_4 grasslands within the individual's home range. The rare earth element (REE) analyses of the gomphothere tusk and the teeth of *Tapirus* and

Teleoceras indicate that these individuals shared similar depositional environments; thus, demonstrating the concurrent presence of C₃ forests and C₄ grasslands. These data therefore support the interpretation of a North American forest refugium in the southern Appalachians during a time typified by more open environments. Additionally, stable carbon and oxygen serial sample variation of less than 1.5‰, suggests minor differences in seasonal temperature and/or precipitation. The high-crowned *Teleoceras* serial samples also had lower variation and overlapped the values of *Floridaceras* from a 15-million year old aseasonal forest in Panama (MacFadden and Higgins, 2004). As the southern Appalachians today are relatively warm and humid at lower elevations with aseasonal precipitation (Sankovski and Pridnia, 1995; Climate Zone, 2006; U.S. Department of Commerce and NOAA, 2006), the Neogene Appalachians may have also served as a thermal refugium to taxa requiring more equable/warmer environments.

In Chapter 4, I first documented the conservative evolution of fossil tapirs and their subsequent diets. Tapir masticatory morphology is consistent with browsing dietary niches through time, despite dramatic global environmental changes during the Cenozoic (Potts and Behrensmeyer, 1992). This is in contrast to closely related, fast-evolving equids (Simpson, 1953; Radinsky, 1984; MacFadden, 1992). Similarly, stable carbon isotope analyses indicate that tapirs have consistently had diets of C₃ vegetation in denser canopied environments than most other sympatric mammalian herbivores. Thus, tapirs are robust indicators of ancient forest habitats and can be used to document how forest distributions have changed over time. After a relatively widespread distribution during the Eocene, declines in tapioroid latitudinal ranges during the Oligocene are consistent with paleobotanical evidence for contracting mesothermal and megathermal vegetation (Potts and Behrensmeyer, 1992; Colbert and Schoch, 1998; Wing, 1998). Tapirs subsequently increase their latitudinal ranges from the Miocene through the

Pleistocene, and recently retreated to occupy only southern distributions below 21° N by ~10,000 years ago, with the most recent contraction likely a result of human activity. Maps of tapiroid (i.e. tapirs and their ancestors) fossil distributions in continental North America provide spatial and temporal proxy evidence for the presence of forest environments.

The work discussed in this dissertation lays the groundwork for interpreting stable isotope data of extinct tapirs through time and understanding how mammalian evolution may have been influenced by an Appalachian forest refugium during the Neogene and forest environments in the New World during the Cenozoic. Future work can instead investigate the paleoecology of tapir dominated environments. Typically, when tapirs are found in the fossil record they are a minor component of the fauna. However, the Gray Fossil Site is a clear exception to this trend (Wallace and Wang, 2004). Since the discovery of the Gray Fossil Site, a second Neogene site with a high proportion of tapir fossils was discovered in north central Florida (Hulbert et al., 2006). This highly fossiliferous Florida fossil site, Haile 7G, is approximately 2 million years old and contains abundant tapirs and xenarthrans, whereas horses and carnivores are rare (Hulbert et al., 2006). Thus, future studies can examine how dietary niches are partitioned within a tapir dominated fauna at Haile 7G, enabling comparisons to the Gray Fossil Site. Such comparisons may provide additional insight into the paleoecology of extinct tapirs and their environments; specifically, clarifying what ecological conditions contribute to the dominance of fossil tapirs and the rarity of typically dominant horses.

Lastly, all of the interpretations of forest environments discussed are based on the work of van der Merwe and Medina (1989, 1991) and others (e.g. Kapos et al., 1993, West et al., 2001) who have documented the relationship between increased canopy density and decreased $\delta^{13}\text{C}$ values in tropical forests. However, little work has been done on documenting how $\delta^{13}\text{C}$

values vary with increased canopy density in temperate forests. Understanding the strength of this relationship and the degree of isotopic variation in temperate forests at various latitudes is critical to proper interpretations of canopy density in the fossil record. Thus, the continued integration of ecological data with paleontological data is required to properly interpret the paleoecology of past environments.

The fossil record can provide valuable insight regarding how environments have changed over time. Modern ecological studies are often limited by time, rarely exceeding one or more decades. Additionally, studies that are of a longer duration are often very costly and logistically difficult. Instead, the fossil record allows long-term ecological questions to be asked that cannot be asked by neontologists. Here, the fossil record helps clarify how forest environments have changed over time. However, our understanding of these forest environments is contingent on understanding extant tapir stable isotope ecology. Thus, the integration of the disparate fields of ecology and paleontology can synergistically improve understandings of past environments and ecological processes through time.

APPENDIX A
IMPORTANCE OF COMMUNICATING THE BROADER IMPACTS OF SCIENTIFIC
RESEARCH TO THE PUBLIC

In the end we will conserve only what we love. We will love only what we understand. We will understand only what we are taught. ~Baba Dioum

Dioum's words, originally addressed to the International Union for Conservation of Nature and Natural Resources, are a personal reminder of the synergistic need for innovative scientific research, quality education, and conservation. As a scientist, educator, and conservationists, I aim to conduct innovative interdisciplinary research, engage in inquiry-based science education, and communicate the conservation implications of my research to the public. Through the education of undergraduate and graduate students, I hope to not only inspire students to pursue careers in the sciences but to also become involved in education and outreach activities that will inspire future generations of scientists.

However, as a graduate student in paleoecology, I have often felt as if I have been in the middle of a tug-of-war with education on one side and science on the other. If I chose to engage in educational activities during my graduate career, my research would consequently receive less attention. Was this okay? Can scientists do both, conduct innovative research and communicate their science to society? I soon realized that not only *can* scientists do both, we *must* do both if we aim to improve scientific literacy. However, it is a constant challenge to figure out the meaning behind broader impact activities and determine how to achieve a necessary balance between research and public outreach.

Currently, the National Science Foundation is attempting to change the culture of ivory tower science, instead requiring scientists to develop a broader impacts component to research grants. One way to excite students about science while extending the reach of scientific grants is to develop educational lessons that communicate actual "hot off the press" research (similar to

that presented in Appendix B). Effective inquiry-based lessons should hook a student's attention and engage them in the process of scientific discovery. In addition, educational models are best disseminated through teacher read educational journals (e.g. the National Association of Biology Teachers and/or the National Association of Science Teacher journals), internet resources, and/or at local or national science teacher meetings. Ideally, scientists should help present an aspect of educational modules in K-12 classrooms. This improves a scientist's ability to communicate complex concepts and concisely explain the importance of their research. Furthermore, it allows students the opportunity to engage in open dialogue with a professional scientist. By infusing young graduate students in the science, technology, engineering, and mathematics (STEM) disciplines into K-12 classrooms, students begin to learn that scientists are represented by individuals from diverse ethnicities and genders.

Participating in outreach that directly extends from current research has been a valued opportunity that I hope all graduate students have the chance to experience, and hopefully something we will all continue with as young professionals. Currently, I aim to continue education and outreach activities associated with ongoing research. In addition, I hope to help future generations of scientific professionals value broader impact activities and gain experience communicating science to the public. By equipping future academics with the skills needed to communicate the broader impacts of scientific research to the public, we will hopefully improve scientific literacy in future generations. Many scientists today have childhood stories that discuss their early passion for discovery. Fostering this innate desire in students of all ages is the responsibility of scientists. For as Diom states, "We will love only what we understand. We will understand only what we are taught."

APPENDIX B
STRAIGHT FROM THE MOUTHS OF HORSES AND TAPIRS: USING FOSSIL TEETH TO
CLARIFY HOW ANCIENT ENVIRONMENTS HAVE CHANGED OVER TIME

Introduction

Do you or your students ever look out the window and imagine prehistoric animals wandering around millions of years ago? Or, when watching movies or shows about the ancient past, do you wonder how scientists know what the environment was like? Clarifying ancient environments millions of years ago is necessary to better understanding how ecosystems change over time, providing insight as to the potential impacts of current global warming. However, understanding how scientists reconstruct past environments is not always straight forward. The activity described here allows students to carry out the same research as professional scientists, develop hypotheses, collect and analyze data, and infer how North American environments have changed over the last 55 million years. Using tooth measurements and dental microwear (i.e. the microscopic wear features that result from the processing of food) methods, students will develop science process skills through the captivating discipline of paleontology.

This module engages middle school students in the scientific process, asking them to test the null hypothesis that horse and tapir diets have not changed over time using tooth measurements (Figure B-1). Based on their tooth study students are then asked to make a new hypothesis regarding the diets of these animals, testing their second hypothesis with dental microwear data. Students utilize multiple learning styles during their paleontology research projects, ultimately making scientific illustrations based on their analysis of quantitative data.

Determining Ancient Diets Using Tooth Morphology

The size and shape of teeth allow paleontologists to interpret the diet of extinct animals based on modern analogues. For example, sharp slicing teeth in lions are used to interpret their dietary strategy as being carnivorous. In contrast, flat blunt teeth as seen in domestic cows are

used for grinding vegetation such as grasses. The proportions of teeth can further elucidate dietary categories by looking at the height of teeth as compared to their anterior to posterior length (i.e. hypsodonty index; Figure B-2; MacFadden, 2000). Modern grazers, such as horses and cows, have high crowned teeth (height > length) that are able to withstand abrasive vegetation including the glass-like silica in grasses. Unlike grazers, living browsers (animals that consume leafy vegetation from trees and shrubs), such as deer and tapirs, typically have low crowned teeth (height < length). With an understanding of how living animal diets relate to tooth shape, we can infer the diet of extinct animals.

Cutting Their Teeth

To begin the activity, provide students with a variety of specimens (e.g. skulls of cows, dogs, cats, horses, etc. – which can be purchased from a biological supply company or borrowed from local museums or universities) or images of skulls (useful images can be found at www.d91.k12.id.us/skyline/teachers/robertsd/mammal1.htm). Ask your students to work in small groups and take ~10 minutes to examine the specimens and figure out what the animals ate. Once students have articulated how they made such inferences, discuss these dietary assignments collectively as a class. Through this opening whole-class discussion students collaboratively inquire as to the diets of the specimens provided, using the shape of teeth to determine if an animal is an herbivore (flat and blunt teeth) or a carnivore (sharp and/or pointy teeth). This discussion provides a necessary lead in to the student's determination of the diets of the fossil animals listed in the data table (Figure B-2) and testing the following hypothesis, "The diets of horses and tapirs have not changed over time."

Collectively as a class, you can introduce and discuss the hypsodonty index (HI) and have them figure out how they might use it to determine if extinct animals ate grasses or leaves. Once students have determined their experimental design together as a class, they can begin

measuring the heights and lengths of the fossil teeth using the Data Sheet provided (Figure B-3). Using the hypsodonty index (HI) ratio, students calculate HI values by simply measuring and then dividing the tooth height by the tooth length for the specimens on their data sheet (Figure B-2, B-3). Once all HI values have been determined, students graph these data points with the age of the fossil as the independent variable (millions of years, x-axis) and HI value as the dependant variable (unit-less ratio, y-axis; Figure B-2). Please note that while Activity Sheet 1 (Figure B-2) gives explicit directions regarding data collection methods, these directions should only serve to refresh students on the experimental design they previously came up with as a class. Next, students can (in small groups of 2–5) evaluate their null hypotheses based on data they collected and graphed. Specifically, students should note that HI values for horses increased approximately 15 million years ago while tapir HI values remained the same over time. This can easily be seen when comparing tapir HI data which forms a straight horizontal line while the horse HI values increase dramatically at ~15 million years ago. Therefore, students can infer that HI values of horses changed over time, likely reflecting a shift in diet from leafy browse to grass. The student's inferences should be discussed collectively as a class, ensuring that everyone thoroughly understands the scientific process and how these data support the conclusions.

Testing Dietary Interpretations with Dental Microwear

Now having a better understanding of the scientific process, data collection, and the graphing of data, students are prepared to embark on their next scientific study in small groups. Based on the results of their tooth morphology study, students develop their second investigation evaluating a new hypothesis with hypothetical microwear data. For example, students can test the hypothesis that the diet of horses changed from that of a browser to a grazer using microscopic marks that result from the processing of food during the animal's lifetime. Because these microscopic features have been studied in living animals with known diets, scientists have

determined that animals with ~1.5 times more “scratches” than “pits” indicate a diet of grass while the reverse is indicative of a diet of leafy browse (MacFadden et al., 1999). By simply counting the “pits” (dots) and “scratches” (lines) on the cartoon microwear slides provided (Figure B-4), student can compare the number of “pits” versus the number of “scratches” to determine how the diets of horses have changed over time. To do this, students should think about their prior study that utilized a ratio of tooth height to length.

In groups, students collaboratively inquire and determine the steps for their study and begin collecting data. In the end, students should plot the relative number of “scratches” vs. “pits” in the form of a ratio referred to as the microwear index (i.e. total number of scratches/total number of pits). If the animal has a microwear index value of greater than 1.5 (1.5 times more scratches than pits) they are inferred to be grazing, while a value of less than 1.5 indicates a browser (MacFadden et al., 1999). Once all data are plotted, students can then test their hypothesis with data demonstrating that horses change from a mixed diet to one of primarily grasses. This evidence subsequently supports the idea that grasslands expanded approximately 20–15 million years ago in North America. Microwear studies provide another line of evidence for looking at how diets of fossil animals have changed over time and can test earlier dietary interpretations as inferred from tooth morphology.

Subsequently, as a class, ask students to interpret how environments have changed over time based on the diets of horses and tapirs. Additionally, ask students to think about some of the problems with their data and what they could do to improve their study. For example, students may mention that by only analyzing the two microwear images provided they may not be capturing what the average horse is eating. This is because each slide is from a different time period, representing only one horse. If this point is not mentioned, students can be asked if they

see any problem with inferring average human diets based on only one person. Students should think about how they could improve their study by increasing the number of microwear images examined for each time period sampled; thus, comparing average values over time (like they did with the tooth morphology study). Lastly, the “last supper” effect of microwear data (i.e. the idea that microwear data captures the last few meals of the animals, as compared to a long-term dietary average) can bias these data. For example, an older horse with worn down teeth may be eating a different diet than it did when it was younger. This issue can be discussed as part of a general wrap-up discussion that focuses on identifying the strengths and weaknesses of the microwear study. Thus, students can discuss ways to improve scientific studies and recognize the benefits of using multiple tools to look at similar questions.

Illustrating and Communicating Scientific Information

After completing the research project described, your students should have an understanding of the scientific process, including how to falsify hypotheses, how sample size plays a role in testing hypotheses, and techniques used to acquire data (i.e. tooth morphology and microwear data). The class discussion mentioned above should be used to assess student understandings thus far. Using their knowledge of the scientific process, their acquired data, and the results of their data analysis, students are now asked to develop an artistic reconstruction of typical horse and tapir environments in North America at ~50 million years ago and also ~5 million years ago. Because both tapirs and horses were browsers ~50 million years ago (based on the first graph of HI values over time), the artistic reconstruction at ~50 million years ago should be of a forest environment. In contrast, the change in horse diets from browsing to grazing ~15 million years ago suggests a ~5 million year old environment as one that has both grasslands and forests. Upon completion of these illustrations, a brief wrap-up discussion should

involve students in recapping how scientific hypotheses were developed, tested, and scientific information interpreted artistically.

Resources

- Fossil Horses in Cyberspace, a web exhibit by the Florida Museum of Natural History where you can learn about paleontology and evolution through fossil horses—
www.flmnh.ufl.edu/fhc
- Megalodon Educator's Guide by the Florida Museum of Natural History contains numerous lessons centered around the largest shark that ever lived, Megalodon—
www.flmnh.ufl.edu/education/guides/megalodon-guide.pdf
- Explorations Through Time by the University of California Museum of Paleontology—
www.ucmp.berkeley.edu/education/explotime.html
- Understanding Evolution for Teachers—evolution.berkeley.edu/evosite/evohome.html
- PBS Evolution Resources—www.pbs.org/wgbh/evolution/index.html



Figure B-1. A student actively measuring fossil horse teeth to test her null hypothesis.

Activity Sheet 1– Reconstructing Ancient Diets Using Tooth Morphology

Paleontologists infer the diets of fossil animals based on their knowledge of living animal diets. For example, grazing horses have high-crowned teeth (the height of the tooth is greater than its length). Their high-crowned teeth are thought to represent an adaptation to the consumption of abrasive vegetation including the glass-like silica in grasses. Unlike horses, tapirs have low-crowned teeth (tooth height is less than the length of the tooth) and eat leafy vegetation from trees and shrubs. Based on the relationships between relative tooth height and diet in living animals, paleontologists can infer the diets of extinct animals.

Today, you will use the same methods as paleontologists to answer the following question:

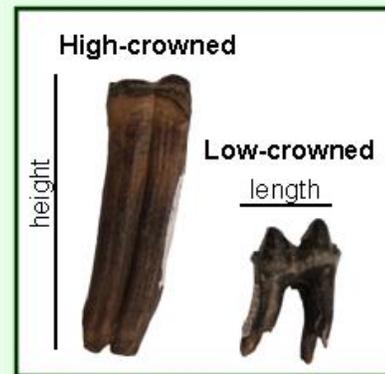
Have the diets of horses and tapirs changed over time – based on their tooth morphology (i.e. tooth shape)?

To answer this question, you must test the null hypothesis that horse and tapir diets have NOT changed over time.

- How can you use the data provided to test this hypothesis (i.e. attempt to falsify the hypothesis)?

Directions

1. Using the tooth images provided, measure the height and length of each tooth, then calculate its hypsodonty index (HI) value (tooth height / tooth length).
2. Once you have measured all of the teeth provided, determine an average HI value for your four horses.
3. Next, graph your data below, adding all of the horse data in the table provided (all of the tapir data is plotted for you – black triangles).



Questions

- Based on the data you graphed, did horse and tapir diets remain the same through time – based on their tooth morphology? Explain.
- Can you falsify this hypothesis? Why or why not?

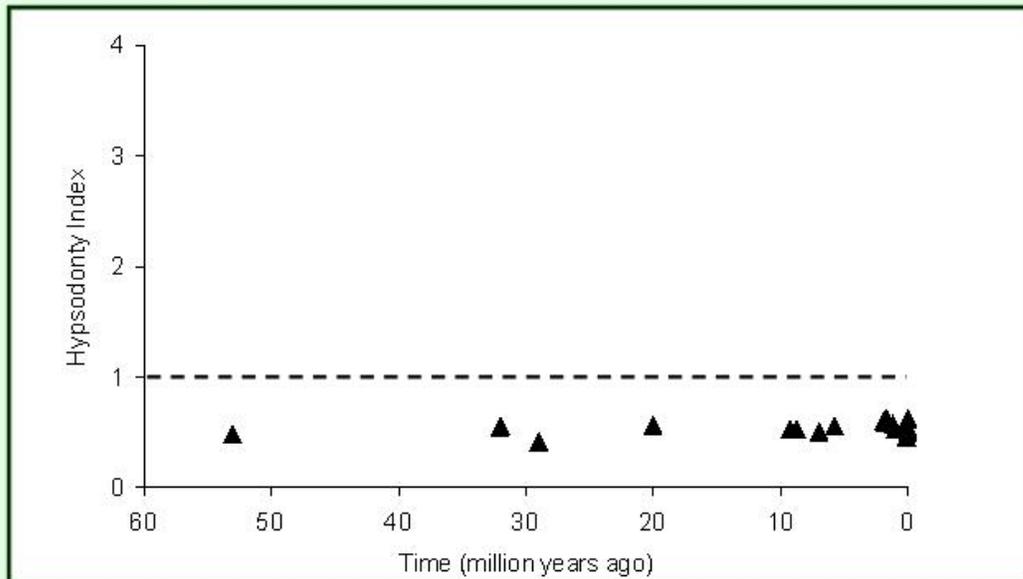


Figure B-2. Activity sheet one allows students to demonstrate how ancient diets can be determined using tooth morphology. All tooth images are from tapir and horse specimens from the Leisey Shell Pit 1A site in Florida, USA.

Data Sheet – Investigating Tooth Morphology

Examine the following teeth and determine their HI value (tooth height / tooth length).

*Note: All of these teeth are approximately 1.5 million years old.



Fossil Horse Data Table

Time (mya)	HI value
55	0.3
55	0.4
53	0.3
53	0.4
51	0.3
51	0.5
51	0.6
50	0.4
50	0.5
49	0.5
45	0.3
45	0.5
33	0.5
30	0.5
25	0.4
25	0.5
20	0.5
19	0.6
19	0.8
18	0.3
18	0.4
18	0.6
17	1.0
15	0.5
15	0.7
15	1.0
15	1.2
15	1.8
12	0.7
12	2.0
12	2.1
10	0.8
5	1.7
5	1.8
5	2.4
0	2.9
0	3.1

Specimen	Tooth height	Tooth length	HI value (height/length)
Tooth A			
Tooth B			
Tooth C			
Tooth D			

Average =

Figure B-3. Data sheet accompanying part one of the activity, includes actual morphological data taken from DeSantis and MacFadden (2007). All tooth images are from tapir and horse specimens from the Leisey Shell Pit 1A site in Florida, USA.

Activity Sheet 2 – Reconstructing Ancient Diets Using Dental Microwear

Based on your recent paleontological study, what did you conclude about the diet of horses and tapirs over time? Do you have any new hypotheses you would like to test? Can dental microwear (microscopic wear features resulting from the processing of food while alive) help you to determine if horses consumed leafy browse versus grass?

Using the data from your tooth morphology study, state a hypothesis you can test (it must be falsifiable) using microwear data.

Hypothesis _____

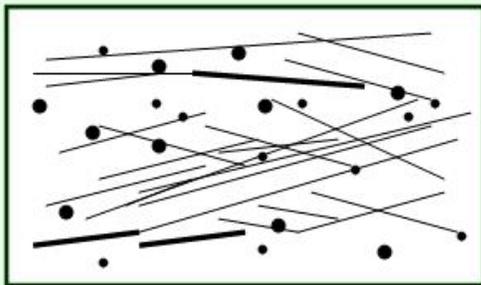
Now, utilize the microwear data below to test this hypothesis.

Directions

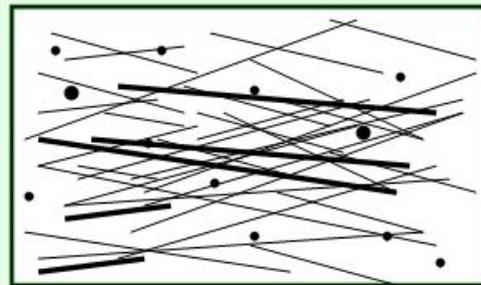
Similar to the HI value, plot your microwear index (MI) value (# of scratches / # of pits) to determine the diet of the fossil and modern horses. Your animal is a grazer if their MI value is greater than 1.5, and a browser if their MI value is less than 1.5.

Determine an effective way to represent this data graphically. Feel free to use examples from your tooth morphology study.

- Do the diets of these horses change through time? Explain.
- How does this data help you to evaluate your hypothesis? Explain.
- What could you do to improve this experiment?



Microwear of a late Miocene (~10 mya) horse, *Cornohipparion*



Microwear of a modern zebra, *Equus burchelli*

Figure B-4. Activity sheet two allows students to demonstrate how ancient diets can be determined using dental microwear. Microwear slides are cartoon reconstructions of SEM microwear images from a fossil and modern horse analyzed by Hayek and others (1991) and cited by MacFadden (2000).

LIST OF REFERENCES

- Baker, G., Jones, L.H.P., Wardrop, I.D., 1959. Cause of wear in sheeps' teeth. *Nature* 4698, 1583-1584.
- BASIN Network, 2006. BASIN Database. Biosphere-Atmosphere Stable Isotope Network. 1 September 2006. <<http://basinisotopes.org/basin/sites/list.html>>
- Bocherens, H., Koch, P.L., Mariotti, A., Geraads, D., Jaeger, J.J., 1996. Isotopic biogeochemistry (^{13}C , ^{18}O) of mammalian enamel from African Pleistocene hominid sites. *Palaios* 11, 306-318.
- Bodmer, R.E., 1990a. Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). *Journal of Zoology* 222, 121-128.
- Bodmer, R.E., 1990b. Responses of ungulates to seasonal inundations in the Amazon floodplain. *Journal of Tropical Ecology* 1990, 191-201.
- Bodmer, R.E., 1991. Influence of digestive morphology on resource partitioning in Amazonian ungulates. *Oecologia* 85, 361-365.
- Brooks, D.M., Bodmer, R.E., Matola, S., 1997. Tapirs: Status Survey and Conservation Action Plan. IUCN/SSC Tapir Specialist Group, Gland.
- Bryant, J.D., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. *Geochimica et Cosmochimica Acta* 59, 4523-4537.
- Bryant, J.D., Luz, B., Froelich, P.N., 1994. Oxygen isotopic composition of fossil horse tooth phosphate as a record of continental paleoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107, 303-316.
- Bryant, J.D., Froelich, P.N., Showers, W.J., Genna, B.J., 1996a. A tale of two quarries: biologic and taphonomic signatures in the oxygen isotope composition of tooth enamel phosphate from modern and Miocene equids. *Palaios* 11, 397-408.
- Bryant, J.D., Froelich, P.N., Showers, W.J., Genna, B.J., 1996b. Biologic and climatic signals in the oxygen isotopic composition of Eocene-Oligocene equid enamel phosphate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 176, 75-89.
- Bryant, J.D., Koch, P.L., Froelich, P.N., Showers, W.J., Genna, B.J., 1996c. Oxygen isotope partitioning between phosphate and carbonate in mammalian apatite. *Geochimica et Cosmochimica Acta* 60, 5145-5148.
- Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120, 347-363.

- Cerling, T.E., Wang, Y., Quade, J., 1993. Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene. *Nature* 361, 344-345.
- Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389, 153-158.
- Cerling, T.E., Harris, J.M., Leakey, M.G., 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. *Oecologia* 120, 364-374.
- Cerling, T.E., Hart, J.A., Hart, T.B. 2004. Stable isotope ecology in the Ituri forest. *Oecologia* 138, 5-12.
- Christie, R.L., McMillan, N.J., 1991. Tertiary Fossil Forests of the geodetic hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin 403, 1-227.
- Clementz, M.T., Koch, P.L., 2001. Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. *Oecologia* 129, 461-472.
- Climate Zone, 2006. Bristol – Johnson City. Climate Zone (www.climate-zone.com). 28 August 2006. <<http://www.climate-zone.com/climate/united-states/tennessee/bristol-johnson-city/>>
- Codron, J., Codron, D., Lee-Thorp, J.A., Sponheimer, M., Bond, W.J., Ruitter, D.D., Grant, R., 2005. Taxonomic, anatomical, and spatio-temporal variations in the stable carbon and nitrogen isotopic compositions of plants from an African savanna. *Journal of Archaeological Science* 32, 1757–1772.
- Colbert, M.W., 2005. The facial skeleton of the Early Oligocene Colodon (Perissodactyla, Tapiroidea). *Palaeontologia Electronica* 8, 12A, 1-27.
- Colbert, M.W., Schoch, R.M., 1998. Tapiroidea and other moropomorphs. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.), *Evolution of Tertiary Mammals of North America 1*. Cambridge Univ. Press, Cambridge, UK, pp. 569-582.
- Coplen, T.B., 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. *Pure and Applied Chemistry* 66, 273-276.
- Crespi, E.J., Rissler, L.J., Browne, R.A., 2003. Testing Pleistocene refugia theory: phylogeographical analysis of *Desmognathus wrighti*, a high-elevation salamander in the southern Appalachians. *Molecular Ecology* 12, 969-984.
- Damuth, J., MacFadden, B.J., 1990. *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge Univ. Press, Cambridge.
- Dansgaard, W., 1964. Stable isotopes in precipitation. *Tellus* 16, 273-276.

- de Candolle, A.P.A., 1874. Constitution dans le règne végétal de groupes physiologiques applicables à la géographie botanique ancienne et moderne. Archives des Science Physiques et Naturelles 50, 5-42.
- DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42, 495-506.
- DeSantis, L.G., MacFadden, B., 2007. Identifying forested environments in Deep Time using fossil tapirs: evidence from evolutionary morphology and stable isotopes. Courier Forschungsinstitut Senckenberg 258, 147-157.
- DeSantis, L.R.G., Feranec, R.S., MacFadden, B.J., 2009. Effects of global warming on ancient mammalian communities and their environments. PLoS ONE 4, e5750.
- Downer, C.C., 1996. The mountain tapir, endangered 'flagship' of the high Andes. Oryx 30, 4458.
- Downer, C.C., 2001. Observations on the diet and habitat of the mountain tapir (*Tapirus pinchaque*). Journal of Zoology 254, 279-291.
- Eberle, J.J., 2005. A new 'tapir' from Ellesmere Island, Arctic Canada – Implications for northern high latitude paleobiogeography and tapir palaeobiology. Palaeogeography, Palaeoclimatology, Palaeoecology 227, 311-322.
- Ehleringer, J.R., Monson, R.K., 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annual Review of Ecology and Systematics 24, 411-439.
- Ehleringer, J.R., Bowling, D.R., Flanagan, L.B., Fessenden, J., Helliker, B., Martinelli, L.A., Ometto, J.P., 2002. Stable isotopes and carbon cycle processes in forests and grasslands. Plant Biology 4, 181-189.
- Eisenberg, J.F., 1981. The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior. Univ. of Chicago Press, Chicago.
- Eisenberg, J.F., 1989. Mammals of the Neotropics: The Northern Neotropics 1. Univ. of Chicago Press, Chicago.
- Feranec, R.S., 2003. Stable isotopes, hypsodonty, and the paleodiet of *Hemiauchenia* (Mammalia: Camelidae): a morphological specialization creating ecological generalization. Paleobiology 29, 230-242.
- Feranec, R.S., 2004. Geographic variation in the diet of hypsodont herbivores from the Rancholabrean of Florida. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 359-369.
- Feranec, R.S., MacFadden, B.J., 2000. Evolution of the grazing niche in Pleistocene mammals from Florida: evidence from stable isotopes. Palaeogeography, Palaeoclimatology, Palaeoecology 162, 155-169.

- Feranec, R.S., MacFadden, B.J., 2006. Isotopic discrimination of resource partitioning among ungulates in C3-dominated communities from the Miocene of California and Florida. *Paleobiology* 32, 191-205.
- Foerster, C.R., Vaughan, C., 2002. Home range, habitat use, and activity of Baird's tapir in Costa Rica. *Biotropica* 34, 423-437.
- Fox, D.L., Fisher, D.C., 2001. Stable isotope ecology of a late Miocene population of *Gomphotherium productus* (Mammalia, Proboscidea) from Port of Entry Pit, Oklahoma, USA. *Palaios* 16, 279-293.
- Fox, D.L., Fisher, D.C., 2004. Dietary reconstruction of Miocene *Gomphotherium* (Mammalia, Proboscidea) from the Great Plains region, USA, based on the carbon isotope composition of tusk and molar enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology* 206, 311-335.
- Fragoso, J.M., 1991. The effect of selective logging on Baird's tapir. In: Mares, M.A., Schmidly, D.J., (Eds.), *Latin American Mammalogy: History, Biodiversity, and Conservation*. Univ. of Oklahoma Press, Norman, OK, pp. 295-304.
- Fricke, H.C., O'Neil, J.R., 1996. Inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: Implication for palaeoclimatological and palaeobiological research. *Palaeogeography, Palaeoclimatology, Palaeoecology* 126, 91-99.
- Galetti, M., Keuroghlian, A., Hanada, L., Morato, M.I., 2001. Frugivory and seed dispersal by the lowland tapir (*Tapirus terrestris*) in southeast Brazil. *Biotropica* 33, 723-726.
- Garten, C.T., Taylor, G.E., 1992. Foliar $\delta^{13}\text{C}$ within a temperate deciduous forest: spatial, temporal, and species sources of variation. *Oecologia* 90, 1-7.
- Graham, A., 1964. Origin and evolution of the biota of southeastern North America: evidence from the fossil plant record. *Evolution* 18, 571-585.
- Graham, A., 1999. *Late Cretaceous and Cenozoic History of North American Vegetation*. Oxford Univ. Press, Oxford.
- Grawe DeSantis, L.R. 2005. Straight from the tapir's mouth: applying stable isotope analyses of extant tapirs to constrain paleoecological hypotheses. In: Kellner, A.W.A., Henriques, D.R. H., Rodrigues, T., (Eds.), *Congresso Latino-Americano de Paleontologia de Vertebrados: Boletim de Resumos 2*. Museu Nacional, Rio de Janeiro, Brazil, pp. 94-95.
- Haffer, J., 1969. Speciation in Amazonian forest birds. *Science* 165, 131-137.
- Haffer, J., Prance, G.T., 2001. Climate forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana* 47, 579-607.

- Hayek, L.A., Bernor, R.L., Solounias, N., Steigerwald, P., 1991. Preliminary studies of hipparionine horse diet as measured by tooth microwear. *Annales Zoologici Fennici* 28, 187-200.
- Henderson, P., Marlow, C.A., Molleson, T.I., Williams, C.T., 1983. Patterns of Chemical Change During Bone Fossilization. *Nature* 306, 358-360.
- Henry, O., Feer, F., Sabatier, D., 2000. Diet of the lowland tapir (*Tapirus terrestris* L.) in French Guiana. *Biotropica* 32, 364-368.
- Higgins, P., MacFadden, B.J., 2004. "Amount Effect" recorded in oxygen isotopes of Late Glacial horse (*Equus*) and bison (*Bison*) teeth from the Sonoran and Chihuahuan deserts, southwestern United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* 206, 337-353.
- Hobson, K.A., Sease, J.L., 1998. Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using Stellar sea lions. *Marine Mammal Science* 14, 116-129.
- Holden, J., Yanuar, A., Marty, D.J., 2003. The asian tapir in Kerinci Seblat National Park, Sumatra: evidence collected through photo-trapping. *Oryx* 37, 34-40.
- Hoppe, K.A., 2006. Correlation between the oxygen isotope ration of North American bison teeth and local waters: implication for paleoclimate reconstructions. *Earth and Planetary Science Letters* 244, 408-417.
- Horrocks, M., Deng, Y., Ogden, J., Sutton, D.G., 2000. A reconstruction of the history of a Holocene sand dune on Great Barrier Island, northern New Zealand, using pollen and phytolith analyses. *Journal of Biogeography* 27, 1269-1277.
- Hulbert, R., Bloch, J., Poyer, A., 2006. Exception preservation of vertebrates from Haile 7G, a new Late Pliocene site from Florida. *Journal of Vertebrate Paleontology* 26, 78A.
- Janis, C.M., 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlations of these factors with dietary preference. In: Russell, D.E., Santoro, J-P., Sigogneau-Russell, D., (Eds.), *Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology*, Paris, Mémoires du Muséum National d'Histoire Naturelle, series C, Paris, pp. 367-387.
- Janis, C.M., Damuth, J., Theodor, J.M., 2000. Miocene ungulates and terrestrial primary productivity: Where have all of the browsers gone? *Proceedings of the National Academy of Sciences* 97, 7899-7904.
- Janis, C.M., Damuth, J., Theodor, J.M., 2002. The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177, 183-198.

- Janis, C.M., Damuth, J., Theodor, J.M., 2004. The species richness of Miocene browsers, and implication for habitat type and primary productivity in the North American grassland biome. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207, 371-398.
- Kapos, V., Ganade, G., Matsui, E., Victoria, R.L., 1993. $\delta^{13}\text{C}$ as an indicator of edge effects in tropical rainforest reserves. *Journal of Ecology* 81, 425-432.
- Klaassen, W., 2001. Evaporation from rain-wetted forest in relation to canopy wetness, canopy cover, and net radiation. *Water Resource Research* 37, 3227–3236.
- Koch, P.L., Tuross, N., Fogel, M.L., 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. *Journal of Archaeological Science* 24, 417-429.
- Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotopic ecology of late Pleistocene mammals in North America: Part 1. Florida. *Chemical Geology* 152, 119-138.
- Koch, P.L., Diffenbaugh, N.S., Hoppe, K.A., 2004. The effects of the late quaternary climate and $p\text{CO}_2$ change on C_4 plant abundance in the south-central United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207, 331-357.
- Kohn, M.J., 1996. Predicting animal $\delta^{18}\text{O}$: accounting for diet and physiological adaptation. *Geochimica et Cosmochimica Acta* 60, 4811-4829.
- Kowalevsky, V., 1873. Sur *L'Anchitherium aurelianense* Cuv. Et sur L'Historie paléontologique des chevaux. *Mém. L' Acad. Impériale Sci. St. Pétersbourg* 7th Sér. (20) 5, 1-73.+
- Krueger, H.W., 1991. Exchange of carbon with biological apatite. *Journal of Archaeological Science* 18, 355-361.
- Lee-Thorp, J.A., van der Merwe, N. J., 1991. Aspects of the chemistry of modern and fossil biological apatites. *Journal of Archaeological Science* 18, 343-354.
- Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. *Proceedings of the National Academy of Sciences* 103, 11201-11205.
- Lizcano, D. J., Cavelier, J., 2004. Características químicas de salados y hábitos alimenticios de la danta de montaña (*Tapirus pinchaque* Roulin, 1829) en los Andes Centrales de Colombia, *Mastozoología Neotropical* 11, 193-201.
- Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a tool for paleohydrological and paleoclimatological research? *Geochimica et Cosmochimica Acta* 48, 385-390.
- MacFadden, B.J., 1986. Fossil horses from “Eohippus” (*Hyracotherium*) to *Equus*: scaling, Cope’s law, and the evolution of body size. *Paleobiology* 12, 355-369.

- MacFadden, B. J., 1992. Fossil Horses: Systematics, Paleobiology, and Evolution of the Family Equidae. Cambridge Univ. Press, Cambridge.
- MacFadden, B.J., 1998. Tale of two rhinos: isotopic ecology, paleodiet, and niche differentiation of *Aphelops* and *Teleoceras* from the Florida Neogene. *Paleobiology* 24, 274-286.
- MacFadden, B.J., 2000. Cenozoic mammalian herbivores from the Americas: reconstructing ancient diets and terrestrial communities. *Annual Review of Ecology and Systematics* 31, 33-59.
- MacFadden, B.J., 2005. Diet and habitat of toxodont megaherbivores (Mammalia, Notoungulata) from the late Quaternary of South and Central America. *Quaternary Research* 64, 113-124.
- MacFadden, B.J., Cerling, T.E., 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: A 10 million-year sequence from the Neogene of Florida. *Journal of Vertebrate Paleontology* 16, 103-115.
- MacFadden, B.J., Shockey, B.J., 1997. Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. *Paleobiology* 23, 77-100.
- MacFadden, B.J., Higgins, P., 2004. Ancient ecology of 15-million-year-old browsing mammals within C₃ plant communities from Panama. *Oecologia* 140, 169-182.
- MacFadden, B.J., Cerling, T.E., Prado, J., 1996. Cenozoic terrestrial ecosystem evolution in Argentina: evidence from carbon isotopes of fossil mammal teeth. *Palaios* 11, 319-327.
- MacFadden, B.J., Solounias, N., Cerling, T.E., 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. *Science* 283, 824-827.
- MacFadden, B.J., Labs-Hochstein, J., Hulbert, R.C., Baskin, J., 2007. Revised age of the late Neogene terror bird (*Titanis*) in North America during the Great American Interchange. *Geology* 35, 123-126.
- McKenna, M.C., Bell, S.K., 1997. Classification of Mammals Above the Species Level. Columbia Univ. Press, New York.
- McLennan, S.M., 1989. Rare Earth Elements in sedimentary rocks; influence of provenance and sedimentary processes. *Reviews in Mineralogy and Geochemistry* 21, 169-200.
- Mendoza, M., Janis, C.M., Palmqvist, P., 2002. Characterizing complex craniodental patterns related to feeding behavior in ungulates: a multivariate approach. *Journal of Zoology* 258, 223-246.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853-858.

- National Climatic Data Center, 2009. Monthly global surface data. 1 May 2009.
<<http://www.ncdc.noaa.gov/oa/ncdc.html>>
- Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Owens, I.P.F., 2005. Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436, 1016-1019.
- Paleobiology Database, 2006. Tapiroidea, Paleobiology Database Online Archives.
<<http://paleodb.org>>
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42.
- Passey, B.H., Cerling, T.E., 2002. Tooth enamel mineralization in ungulates: Implications for recovering a primary isotopic time-series. *Geochimica et Cosmochimica Acta* 66, 3225-3234.
- Passey, B.H., Cerling, T.E., Perkins, M.E., Voorhies, M.R., Harris, J.M., Tucker, S.T., 2002. Environmental change in the Great Plains: an isotopic record from fossil horses. *Journal of Geology* 110, 123-140.
- Patrick, D., Terry Jr., D.O., Grandstaff, D.E., 2001. Rare earth element (REE) variation in fossil and modern bones: the influence of osteological materials and time. *Geological Society of America Abstracts with Programs* 33, 27.
- Poage, M.A., Chamberlain, C.P., 2001. Empirical relationships between elevation and the stable isotope composition of precipitation and surface waters: considerations for studies of paleoelevational change. *American Journal of Science* 301, 1-15.
- Post, E., Forchhammer M.C., 2004. Spatial synchrony of local populations has increased in association with the recent Northern Hemisphere climate trend. *Proceedings of the National Academy of Sciences* 101, 9286-9290.
- Potts, R., Behrensmeyer, A.K., 1992. Late Cenozoic terrestrial ecosystems. In: Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H-D., Wing, S.L. (Eds.), *Terrestrial Ecosystems Through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals*. Univ. of Chicago Press, Chicago, pp. 419-541.
- Quade, J., Cerling, T.E., Barry, J.C., Morgan, M.E., Pilbeam, D.R., Chivas, A.R., Lee-Thorp, J.A., van der Merwe, M.J. 1992. A 16-Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. *Chemical Geology* 94, 183-192.
- Radinsky, L.R. 1984. Ontogeny and phylogeny in horse skull evolution. *Evolution* 38, 1-15.
- Retallack, G.J., 2001. Cenozoic expansion of grasslands and climatic cooling. *Journal of Geology* 109, 407-426.

- Roux, X.L., Bariac, T., Sinoquet, H., Genty, B., Piel, C., Mariotti, A., Girardin, C., Richard, P., 2001. Spatial distribution of leaf water-use efficiency and carbon isotope discrimination within an isolated tree crown. *Plant, Cell and Environment* 24, 1021-1032.
- Salas, L.A., 1996. Habitat use by lowland tapirs (*Tapirus terrestris* L.) in the Tabaro River Valley, southern Venezuela. *Canadian Journal of Zoology* 74, 1452-1458.
- Salas, L.A., Fuller, T.K., 1996. Diet of the lowland tapir (*Tapirus terrestris* L.) in the Tabaro River Valley, southern Venezuela. *Canadian Journal of Zoology* 74, 1444-1451.
- Sánchez, B., Prado, J.L., Alberdi, M.T., 2003. Paleodiet, ecology, and extinction of Pleistocene gomphotheres (Proboscidea) from the Pampean Region (Argentina). *Coloquios de Paleontología* 1, 617-625.
- Sánchez, B., Prado, J.L., Alberdi, M.T., 2004. Feeding ecology, dispersal, and extinction of South American Pleistocene gomphotheres (Gomphotheriidae, Proboscidea). *Paleobiology* 30, 146-161.
- Sankovski, A., Pridnia, M., 1995. A comparison of the Southern Appalachians (U.S.A.) and Southwestern Caucasus (Russia) forests: influences of historical events and present environments. *Journal of Biogeography* 22, 1073-1081.
- Schubert, B., Wallace, S., 2006. Amphibians and reptiles of the Mio-Pliocene Gray Fossil Site and their paleoecological implications. *Journal of Vertebrate Paleontology* 26, 122A.
- Shunk, A.J., Driese, S.G., Clark, G.M., 2006. Latest Miocene to earliest Pliocene sedimentation and climate record derived from paleosinkhole fill deposits, Gray Fossil Site, northeastern Tennessee, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology* 231, 265-278.
- Simpson, G.G., 1953. *The Major Features of Evolution*. Columbia Univ. Press, New York.
- Solounias, N., Moelleken, S.M.C., 1993. Dietary adaptation of some extinct ruminants determined by premaxillary shape. *Journal of Mammalogy* 74, 1059-1071.
- Sponheimer, M., Lee-Thorp, J.A., 1999. Oxygen isotopes in enamel carbonate and their ecological significance. *Journal of Archaeological Science* 26, 723-728.
- Stehli, F.G., Webb, S.D., 1985. *The Great American Biotic Interchange*. Plenum Press, New York.
- Stromberg, C.A.E., 2005. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the National Academy of Sciences* 102, 11980-11984.
- Stuwe, M., Abdul, J.B., Nor, B.M., Wemmer, C.M., 1998. Tracking the movements of translocated elephants in Malaysia using satellite telemetry. *Oryx* 32, 68-74.

- Terwilliger, V.J., 1978. Natural history of Baird's tapir on Barro Colorado Island, Panama Canal Zone. *Biotropica* 10, 211-220.
- Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., Slade, N.A., 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57, 32-37.
- Tobler, M.W., 2002. Habitat use and diet of Baird's tapirs (*Tapirus bairdii*) in a montane cloud forest of the Cordillera de Talamanca, Costa Rica. *Biotropica* 34, 468-474.
- Todd, N., 2006. Trends in Proboscidean diversity in the African Cenozoic. *Journal of Mammalian Evolution* 13, 1-10.
- Trueman, C.N., 1999. Rare Earth Element geochemistry and taphonomy of terrestrial vertebrate assemblages. *Palaaios* 14, 555-568.
- Trueman, C.N.G., Behrensmeyer, A.K., Tuross, N., Weiner, S., 2004. Mineralogical and compositional changes in bone exposed on soil surfaces in Amboseli National Park, Kenya: diagenetic mechanisms and the role of sediment pore fluids. *Journal of Archaeological Sciences* 31, 721-739.
- Tu, T.T.N., Kürschner, W.M., Schouten, S., Van Bergen, P.F., 2004. Leaf carbon isotope composition of fossil and extant oaks grown under differing atmospheric CO_2 levels. *Palaeogeography, Palaeoclimatology, Palaeoecology* 212, 199-213.
- U.S. Department of Commerce and National Oceanic and Atmospheric Administration, 2006. Get/View on-line climate data. NOAA Satellite and Information Service and National Climatic Data Center. 28 August 2006 <<http://www.ncdc.noaa.gov/oa/climate/climatedata.html>>
- van der Merwe, N.J., Medina, E., 1989. Photosynthesis and $^{13}\text{C}/^{12}\text{C}$ ratios in Amazonian rain forests. *Geochimica et Cosmochimica Acta* 53, 1091-1094.
- van der Merwe, N.J., Medina, E., 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *Journal of Archaeological Science* 18, 249-259.
- Wallace, S.C., Wang, X., 2004. Two new carnivores from an unusual late Tertiary forest biota in eastern North America. *Nature* 431, 556-559 + Supplement
- Walter, R., Epperson, B.K., 2005. Geographic pattern of genetic diversity in *Pinus resinosa*: contact zone between descendants of glacial refugia. *American Journal of Botany* 92, 92-100.
- Walther, G-R., Post, E., Convey, P., Menzel A., Parmesan, C., Beebee, T.J.C., Fromentin, J-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389-395.

- Wang, Y., Cerling, T.E., MacFadden, B.J., 1994. Fossil horses and carbon isotopes: new evidence for Cenozoic dietary, habitat, and ecosystem changes in North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107, 269-279.
- Waterisotopes.org, 2006. OIPC, The online isotopes in precipitation calculator. Waterisotopes.org. 28 August 2006. <http://wateriso.eas.purdue.edu/waterisotopes/pages/data_access/oipc.html>
- West, A.G., Midgley, J.J., Bond, W.J., 2001. The evaluation of $\delta^{13}\text{C}$ isotopes of trees to determine past regeneration environments. *Forest Ecology and Management* 147, 139-149.
- Wing, S.L., 1998. Tertiary vegetation of North America as a context for mammalian evolution. In: Janis, C.M., Scott, K.M., Jacobs, L.L., (Eds.), *Evolution of Tertiary Mammals of North America 1*. Cambridge Univ. Press, Cambridge, UK, pp. 37-65.
- Wing, S.L., Harrington, G.J., Smith, F.A., Bloch, J.I., Boyer, D.M., Freeman, K.H., 2005. Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* 310, 993-996.
- Wing, S.L., Sues, H.D., 1992. Mesozoic and early Cenozoic terrestrial ecosystems. In: Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H-D., Wing, S.L., (Eds.), *Terrestrial Ecosystems Through Time: Evolutionary Paleocology of Terrestrial Plants and Animals*. Univ. of Chicago Press, Chicago, pp. 327-416.
- Wolfe, J.A., 1975. Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary. *Annals of the Missouri Botanical Garden* 62, 264-279.
- Wolfe, J.A., 1994. Tertiary climatic changes at middle latitudes of western North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108, 195-205.
- Zazzo, A., Mariotti, A., Lécuyer, C., Heintz, E., 2002. Intra-tooth isotope variations in late Miocene bovid enamel from Afghanistan: paleobiological, taphonomic, and climatic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 186, 145-161.

BIOGRAPHICAL SKETCH

Larisa R. G. DeSantis, a Los Angeles native born in 1979, has had a passion for discovery and the outdoors since childhood. Always asking, “why and how,” she became fascinated with earth’s current and past inhabitants and enrolled in her first dinosaur class at the Los Angeles Natural History Museum at the age of 6. She began studying paleobiology during her freshman year at the University of Chicago in 1997. In 2000, she earned a Bachelor of Science degree in Resource Management with double honors from the University of California, Berkeley. She later went on to earn a Master in Environmental Management degree at Yale University in 2003. While at Yale, she was active in museum education and outreach through the Yale Peabody Museum. Subsequently, she accepted a position with the American Museum of Natural History in New York City, driving a 38-ft Paleontology of Dinosaurs Moveable Museum where she educated students and the public about paleontology. Determined to integrate her passions for paleontology and ecology, she moved to Gainesville, Florida in 2004 where she began her doctorate studying the paleoecology of ancient forests and their mammalian inhabitants. While at the University of Florida she maintained involvement in numerous educational outreach programs and completed her doctoral research in 2009. Currently, she is an Assistant Professor in the Department of Earth and Environmental Sciences at Vanderbilt University.