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# Middle Miocene Paleoenvironmental Reconstruction of the Central Great Plains from Stable Carbon Isotopes in Large Mammals

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MIDDLE MIOCENE PALEOENVIRONMENTAL RECONSTRUCTION  
OF THE CENTRAL GREAT PLAINS FROM STABLE CARBON  
ISOTOPES IN LARGE MAMMALS

by

Willow H. Nguy

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Major: Earth and Atmospheric Sciences

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July, 2017

# MIDDLE MIOCENE PALEOENVIRONMENTAL RECONSTRUCTION OF THE CENTRAL GREAT PLAINS FROM STABLE CARBON ISOTOPES IN LARGE MAMMALS

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University of Nebraska, 2017

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Middle Miocene (18-12 Mya) mammalian faunas of the North American Great Plains contained a much higher diversity of apparent browsers than any modern biome. This has been attributed to greater primary productivity, which may have supported greater browser diversity that commonly corresponds with densely vegetated habitats. However, several lines of proxy evidence suggest that open woodlands or savannas dominated middle Miocene biomes; neither of which support many browsers today. Stable carbon isotopes in mammalian herbivore tooth enamel were used to reconstruct vegetation structure of middle Miocene biomes.

Stable carbon isotopes in  $C_3$  dominated environments reflect vegetation density and herbivores in those environments record dietary values of vegetation in their tissues with predictable offsets. Tooth enamel was sampled from presumed browsers, mixed-feeders, and grazers, based on hypsodonty and microwear studies, from four late Barstovian (14.8-12.5 Mya) localities in Nebraska. Paleoenvironmental interpretations were made using a predictive model based on  $\delta^{13}C$  values in  $C_3$  vegetation in modern biomes. The model adjusts for differences in atmospheric  $\delta^{13}C$  between the Barstovian and present, diet-to-enamel enrichment, and latitudinal and altitudinal differences in  $\delta^{13}C$  plant values.

Mean  $\delta^{13}C$  faunal values plot in the upper range of values expected for  $C_3$  vegetation, suggesting open habitats. Means for several taxa plot in the range for water-

stressed C<sub>3</sub> environments; a range that overlaps partially with the range for C<sub>4</sub> vegetation. One individual has a high enough value to unequivocally indicate C<sub>4</sub> consumption ( $\delta^{13}\text{C}=-6.0$ ). The taxa that plot in the water-stressed range could potentially indicate up to 5% total C<sub>4</sub> consumption, but this is lower than estimates made from paleosol carbonates that suggest 20% mean C<sub>4</sub> biomass at this time. The narrow range in carbon isotope values suggests that browsers, mixed feeders, and grazers all consumed vegetation in mostly open areas. These results are consistent with other proxy data suggestive of savanna-woodland biomes during the middle Miocene, despite high browser diversity, which does not appear to have a modern analogue.

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## 1. INTRODUCTION

During the late Neogene (~8 to 3 Mya), many global environments were transformed from landscapes dominated by plants utilizing C<sub>3</sub> photosynthesis into grasslands employing C<sub>4</sub> photosynthesis (Edwards *et al.* 2010). This change is reflected in notable positive shifts in stable carbon isotope values in both paleosol carbonates and mammalian herbivore enamel as <sup>13</sup>C-enriched C<sub>4</sub> plants increased in biomass and mammals consumed increasing amounts of C<sub>4</sub> grasses (Cerling *et al.* 1993; Wang *et al.* 1994; Cerling *et al.* 1997). The paleobotanical microfossil record records this increase in C<sub>4</sub> vegetation by an increase in grass phytoliths (Strömberg and McInerney 2011). Some authors suggest that C<sub>4</sub> vegetation started as geographically isolated pockets and persisted for long periods before this sudden expansion, unlike earlier hypotheses of a sudden global takeover (Christin *et al.* 2008; Vicentini *et al.* 2008; Feranec and Pagnac 2013). A study of carbon isotopes in paleosol carbonates suggested that 12-34% (mean=20%) of C<sub>4</sub> biomass was already present in the early Miocene of North America (Fox and Koch 2004). Furthermore, paleobotanical phylogenetic studies have suggested that C<sub>4</sub> vegetation originated earlier than the Early Oligocene (Christin, *et al.* 2008; Vicentini *et al.* 2008). However, mammalian faunal isotope studies suggest that, if C<sub>4</sub> vegetation was present, very few mammalian taxa were consuming (Passey *et al.* 2002; MacFadden and Higgins 2004; Secord *et al.* 2008; Boardman and Secord 2013; Kita *et al.* 2014).

Other authors have suggested that grasslands were not a new feature, and that C<sub>3</sub> grasslands were an important biome since the Oligocene and a determining factor in the increase in grazer diversity before the expansion of C<sub>4</sub> grasslands (Stebbins 1981; MacFadden 1997; Fox and Koch 2003). Studies of phytolith concentrations suggest

mosaics of grasslands and forests as early as the early Miocene (Strömberg 2002, 2004, 2005). However, during the middle Miocene (18-12 Mya) in North America, browsing ungulates reached a peak in diversity with up to three times the number of browsing species present in modern biomes (Janis *et al.* 2000, 2004). This non-analog peak in browser diversity must have been supported by a vast amount of browse, but some evidence suggests that middle Miocene biomes of North America were fairly open environments, possibly analogous to modern savannas or woodlands (Axelrod 1985; Retallack 2001; Janis *et al.* 2004; Fox and Koch 2004; Strömberg 2004). The transition from browsing to grazing in the Great Plains is best known in equids from faunal isotopes and changes in hypsodonty indices (Wang *et al.* 1994; Passey *et al.* 2002; Strömberg 2006), but this transition is not well studied in many other Miocene ungulates, beyond comparisons of simple hypsodonty indices (Janis *et al.* 2000, 2004).

This study samples a large diversity of Perissodactyls and Artiodactyls, many of which have sparse stable isotope records, to examine the dietary niches of ungulates present and to create a new and more complete record of faunal isotopes in the middle Miocene of the Great Plains. This study uses stable carbon isotopes from mammalian herbivore tooth enamel to infer the vegetation density and to reconstruct the paleoenvironment of the late middle Miocene.

The reconstruction of middle Miocene paleoenvironments is important for understanding the transition from forests to grasslands across the Great Plains and for understanding the environment that supported the elevated browser diversity at this time.

This study seeks to address the following questions: (1) Were ungulates in the middle Miocene consuming predominantly C<sub>3</sub> vegetation? (2) Was the middle Miocene

(Barstovian) biome characterized by open habitats, closed forests, or a patchwork of both? (3) Did the peak in browser diversity in the middle Miocene correspond with browsers partitioning resources in heavily vegetated areas? And (4) Was there a detectable change in the biome between the Barstovian and the Clarendonian, when browser diversity began to decline?

## 2. BACKGROUND

### 2.1 Geologic Context

Fossil localities used in this study are distributed as shown in Fig. 1. All faunas were correlated to the late Barstovian (Ba2: 14.8- 12.5 Mya, Tedford *et al.* 2004) biochron of the Barstovian North American Land Mammal Age (NALMA) by Voorhies (1990a). The late Barstovian is based upon the first appearance of the *Gomphotheriidae* and is supported by the presence of the taxa *Plihippus*, *Neohipparion*, *Cormohipparion*, *Ustatochoerus medius*, *Longirostromeryx* and many others not used in this study (Tedford *et al.* 2004). It is also characterized by the last occurrences of *Ticholeptus*, *Pseudoparablastomeryx*, and *Bouromeryx* (Tedford *et al.* 2004).

The localities used in this study occur in the Cornell Dam and overlying Crookston Bridge members of the Valentine Formation of the Ogallala Group, and are characterized by fluvial deposits containing fossiliferous, semiconsolidated silty sandstones, cross-bedded sandstones, and conglomeratic layers (Skinner and Johnson 1984; Voorhies 1990b). Valentine Formation rocks of Ba2 unconformably overlie the Oligocene Rosebud Formation (Voorhies 1990b).

The basal Cornell Dam Member was deposited above the unconformity and contains the Hottell Ranch Rhino Quarry, the Immense Journey Quarry (Voorhies *et al.* 1987), and the Norden Bridge Quarry (Voorhies 1990b). The Hottell Ranch Rhino Quarry and the Immense Journey Quarry faunas are referred to here as the Hottell Ranch/Immense Journey (HI) local fauna whereas faunas from Norden Bridge Quarry are referred to as the Norden Bridge (NB) local fauna. The ages of the local faunas used in this study can be further constrained by the Hurlbut Ash, which sits above the Norden

Bridge Quarry. It has been dated at  $13.55 \pm 0.09$  Mya by  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of glass (Swisher 1992) and  $13.5 \pm 0.1$  Mya by interpolation of magmatic stage composition (Perkins and Nash 2002) and limits the Hottell Ranch/Immense Journey and Norden Bridge local faunas to 14.8-13.6 Mya.

The Crookston Bridge Member of the Valentine Formation sits conformably above the Cornell Dam Member and contains the Type Valentine Quarry, West Valentine Quarry, and Railway “b” Quarry (Holman and Sullivan 1981). The faunas from the Type Valentine Quarry, the West Valentine Quarry, and the Railway “b” Quarry are referred to here as the Valentine Quarry local fauna. This local fauna occurs above the Hurlbut Ash (13.55Mya) and below the Swallow Ash in the overlying Ash Hollow Formation, which has been dated at  $12.2 \pm 0.12$  Mya by  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of glass (Swisher 1992), however, the distinct separation between faunas of Barstovian and Clarendonian ages lowers this boundary to  $12.5 \pm 0.1$  Mya based upon the Cronese Tuff (Tedford *et al.* 2004) at the base of the Dove Springs Formation in California. This constrains the Valentine Quarry local fauna to 13.6-12.5 Mya.

## *2.2 Carbon Isotopes in Mammals*

Mammalian herbivores acquire carbon by ingesting plant material. Metabolism and biomineralization fractionates stable carbon isotopes from these plants with a predictable offset (enrichment factor; Cerling and Harris 1999; Passey *et al.* 2005). The nature of the diet-tissue relationship allows the carbonate in mammalian herbivore enamel to be used to estimate the bulk diet of fossil mammals (DeNiro and Epstein 1978; Cerling and Harris 1999).



This relationship can be used to tell whether a mammal was consuming primarily  $C_4$  vegetation,  $C_3$  vegetation, or a mixture of both. Mammals that consume purely  $C_4$  vegetation have much more positive carbon isotope values than mammals that consume purely  $C_3$  vegetation (Vogel 1978; MacFadden and Cerling 1994). These endmember diets have very little overlap in their isotopic ranges, so intermediate values are indicative of a mixed diet or, in limited instances, CAM (Crassulian Acid Metabolism) vegetation (MacFadden and Cerling 1996; Cerling *et al.* 1997). Plants using CAM photosynthesis include succulents that grow primarily in very arid environments (Ehleringer *et al.* 1991). The biomes these faunas inhabited are interpreted to be sub-humid by floral and paleosol studies (MacGinitie 1962; Retallack 1997), so CAM vegetation is not considered to be a major dietary component in this study.  $C_3$  plants occupy a variety of biomes ranging from rainforests to woodlands to savannas and grasslands, whereas  $C_4$  vegetation usually occurs as grasses in open, seasonally dry biomes. Studies have shown that most terrestrial environments at mid-latitudes before the expansion of  $C_4$  grasslands were dominated by  $C_3$  vegetation (Cerling *et al.* 1993; Quade and Cerling 1995). However, some studies suggest that considerable  $C_4$  biomass (12-34% mean=20%) was present in the early and middle Miocene (Fox and Koch 2004).

The vegetation density of  $C_3$  biomes can be also be interpreted with carbon isotope values, and thus, can be used to infer an herbivore's corresponding biome. Mammals that consume  $C_3$  plants that grow in an area where water is readily available have lower carbon signatures than where plants are water stressed. Generally, carbon isotopes in plants become more negative with increasing rainfall (Stewart *et al.* 1995; Schulze *et al.* 1998). Mammals that consume plants grown in shade or under a closed

canopy, rather than in open sunshine, will also have more negative signatures due to slower photosynthetic rates (Ehleringer *et al.* 1986; van der Merwe and Medina 1991; Graham *et al.* 2014). These environmental trends in C<sub>3</sub> vegetation mean that mammalian herbivores consuming plants in wet, closed environments will have more negative isotopic signatures than herbivores consuming plants in drier, open environment, assuming that modern diet-to-enamel enrichment factors can be applied directly into the past (Koch 1998; Cerling and Harris 1999; Feranec and MacFadden 2006; Secord *et al.* 2008). Although these trends are helpful in distinguishing between open and closed environments, distinguishing between types of C<sub>3</sub> vegetation is not possible. For example, a mammal eating C<sub>3</sub> grass in a bright, open area can have a similar signature to a mammal eating C<sub>3</sub> browse in the same area. This study assumes that faunas with signatures in the upper range predicted for C<sub>3</sub> biomes reflect the consumption of plants in a woodland savanna-like environment. Here I use woodland savanna to encompass a range of possible biomes referring to the gradient between woodlands (less than 80% tree cover, but with a broken canopy), shrublands (dominated by small-medium woody plants), and wooded savannas (less than 40% tree cover and a continuous herbaceous layer containing grasses).

### 2.3 Oxygen Isotopes in Mammals

Stable oxygen isotopic composition of mammalian herbivore enamel also reflects environmental factors. Oxygen isotopes in mammal tissues are derived from ingested water, metabolic water, and water vapor from the atmosphere (Bryant and Froelich 1995). These isotopes are fractionated between the generally constant physiological <sup>18</sup>O-enrichment between body water and tissues and taxonomic differences in physiology

(Bryant and Froelich 1995; Kohn 1996; Kohn *et al.* 1996). Differences in the physiological fractionation can help to identify different strategies in water usage among taxa.

All ingested water is ultimately derived from precipitation, but mammals acquire their water from sources with different histories of fractionation. Within localities, mammals that have different hydration requirements will have differing relative isotopic signatures. Herbivores that derive most of their ingested water from vegetation or that are drought-tolerant tend to have higher  $\delta^{18}\text{O}$  values. This is because leaf-water is  $^{18}\text{O}$ -enriched by evaporation and  $\delta^{18}\text{O}$  values in plants increase with decreasing water-availability and increasing aridity (Yakir *et al.* 1990; Levin *et al.* 2006). In contrast, mammals that are water-dependent, obligate drinkers, have lower isotope values because their ingested water is derived more directly from precipitation (Bryant and Froelich 1995; Kohn 1996). Taxa within a local fauna that have relatively high oxygen isotope values may be indicative of open areas where irradiance causes more evaporation and therefore an enrichment in  $^{18}\text{O}$  (Quade *et al.* 1995; Cerling *et al.* 2004; Boardman and Secord 2013).

### 3. METHODS

#### *3.1 Sample Selection*

This study includes bulk enamel samples of 126 teeth encompassing 27 genera from the three local faunas. Specimens are curated in the Division of Vertebrate Paleontology at the University of Nebraska State Museum (UNSM). Most initial identifications were done by M.R. Voorhies or R.G. Corner. Identifications were further checked by comparison with casts of holotypes (when available) and published taxonomic descriptions. The families and genera from the local faunas are listed in Table 1. Taxa were selected that were most representative of the local fauna. Effort was made to sample common taxa to capture the general biome and any uncommon or rare taxa to capture the range of habitats present.

#### *3.2 Sampling and Pretreatment*

To avoid damaging important specimens for taxonomic studies, teeth or fragmentary jaws were preferentially chosen. First molars and deciduous teeth were not used to avoid potential weaning signals (Jenkins et al. 2001; Balasse 2001; Rountrey et al. 2007). Late erupting teeth that capture an adult diet, such as third molars and fourth premolars (Hillson 2005), were given preference, but second molars and third premolars were also sampled when others were unavailable. Care was taken to only sample pristine enamel without discolored or decalcified spots or cracks.

Using PlatSil® silicone rubbers and TAP® Four-to-One epoxy resin, molds and casts were made of uncommon or fragile specimens to preserve morphology for future researchers.

Bulk enamel samples were collected under a binocular microscope using a mounted, NSK®, variable speed dental drill with 1 mm diamond burrs. For each specimen, approximately 4 mg of enamel was drilled along a non-occlusal surface perpendicular to the tooth's growth axis to obtain a time-averaged sample.

Powdered enamel samples were then pretreated following Koch and others (1997). To remove organic matter, samples were treated with a 3% NaOCl solution for 24 hours, rinsed with deionized water five times, and dried for 10-12 hours in a 60°C oven. To remove nonstructural carbonates, samples were then treated with a solution of 1 M acetic acid with calcium acetate as a buffer for 24 hours and rinsed five times with deionized water. Instead of lyophilizing the samples as suggested in Koch and others (1997), samples were dried for at least 12 hours at 60°C to remove excess water.

### *3.3 Isotopic Analysis*

Pretreated samples were sent to the University of Michigan Stable Isotope Laboratory (UMSIL) for stable isotope analysis. CO<sub>3</sub> in the enamel samples was converted to CO<sub>2</sub> in a Finnigan MAT Kiel IV preparation device by reacting the samples with H<sub>3</sub>PO<sub>4</sub> for 17 minutes at 77±1°C. A Finnigan MAT 253 triple collector isotope ratio mass spectrometer was used to measure the isotopic ratios of the CO<sub>2</sub>. For both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  at UMSIL, analytical precision is better than ±0.1‰ (1 $\sigma$ ) at UMSIL (Lora Wingate, lab manager- pers. comm. 2017) based on international standards for carbonate (NBS-18 and NBS-19). An intra-lab enamel standard was included with each batch of enamel samples to control variance among batches. MES (a fossil mammoth standard from New Mexico) had a mean value and variance of  $\delta^{13}\text{C} = -9.67 \pm 0.02\text{‰}$  and  $\delta^{18}\text{O} = 23.17 \pm 0.10\text{‰}$ .

(1 $\sigma$ , n=15), which agrees closely with previous runs at UMSIL ( $\delta^{13}\text{C} = -9.67 \pm 0.03\%$ ;  $\delta^{18}\text{O} = 23.19 \pm 0.22\%$ ; 1 $\sigma$ , n=27).

Isotopic ratios are presented as standard  $\delta$ -notation where  $\delta X = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000$ . Here, X represents the  $^{13}\text{C}$  or  $^{18}\text{O}$  value and R represents  $^{13}\text{C}/^{12}\text{C}$  or  $^{18}\text{O}/^{16}\text{O}$ , respectively. Here,  $\delta^{13}\text{C}$  values are reported relative to the Vienna PeeDee Belemnite (VPDB) standard and  $\delta^{18}\text{O}$  values are reported relative to the Vienna Standard Mean Ocean Water (VSMOW) standard.

Errors on mean values in the rest of this paper are reported as 95% confidence of the mean  $\left( 1.96 \times \frac{\text{standard deviation}}{\sqrt{n-1}} \right)$ .

### 3.4 Predicting carbon isotope values for middle Miocene mammals

To predict  $\delta^{13}\text{C}$  values for mammalian ungulates feeding in a variety of possible Barstovian biomes, a model was created following the examples of Secord and others (2008), Boardman and Secord (2013), and Kita and others (2014). This model used  $\delta^{13}\text{C}$  values of modern vegetation to characterize a full range of habitats from dense, closed canopy rainforests to open  $\text{C}_3$  woodlands to  $\text{C}_4$  grasslands. The values for these biomes were normalized to middle Miocene Nebraska by accounting for the following factors:

1. Vegetation receiving the equivalent light and water have  $\delta^{13}\text{C}$  values that differ based on the latitude at which the plants grew (Körner *et al.* 1991.) This adjustment was an increase of approximately  $0.3\%/10^\circ$  latitude (Secord *et al.* 2008), so all habitats were adjusted to  $40.9^\circ \text{ N}$ , the average paleolatitude of the localities included in the study (Douwe *et al.* 2015).

2. Vegetation at different altitudes receiving equivalent light and water also return different  $\delta^{13}\text{C}$  values. Because the area has not experienced any major orogenic uplift since deposition, habitats were normalized to 0.86 km, the average modern altitude of the localities. This was achieved by applying an increasing adjustment of 0.65‰/1000m (Secord *et al.* 2008 calculated from Körner *et al.* 1988)
3. Carbon isotope values in atmospheric  $\text{CO}_2$ , estimated from benthic foraminifera (Tippie *et al.* 2010) suggest the late Barstovian atmosphere was approximately 0.48‰ more positive than the present. A second increase of 1.5‰ was made to account for the  $^{13}\text{C}$ -depleting effects of industrialization and the use of fossil fuels (Friedli *et al.* 1986). In total, a positive atmospheric adjustment of 1.98‰ was made to the model.
4. To adjust for diet-enamel enrichment, an enrichment factor ( $\epsilon^*$ ) of  $14.1 \pm 0.5\%$  ( $1\sigma$ ) was applied based on African ruminant and non-ruminant ungulates (Cerling and Harris 1999). As this study included a diversity of perissodactyls and artiodactyls, this average ungulate diet-enamel enrichment should be appropriate to compensate for physiological differences.

Using these adjustments, boundaries for middle Miocene biome  $\delta^{13}\text{C}$  values were identified. Closed  $\text{C}_3$  canopy biomes (rainforest and dense monsoonal forest):  $\leq -13.1\%$ ; open  $\text{C}_3$  canopy biomes (“wet” and “dry” deciduous forest, “dry” tropical forest, woodland, shrubland, savanna, and  $\text{C}_3$  grassland):  $> -13.1\%$  to  $\leq -7.0\%$ ; mixed  $\text{C}_3/\text{C}_4$  biomes:  $> -7.0\%$  to  $\leq 1.7\%$ ; and pure  $\text{C}_4$  grasslands:  $> 1.7\%$ .

Mammals reporting carbon values towards the upper ranges of open  $\text{C}_3$  biomes could be consuming small amounts of  $\text{C}_4$  vegetation. This study examines the

paleoenvironment of the late Barstovian, nearly seven million years before the expansion of C<sub>4</sub> grasslands, and it is assumed that these environments were dominated by C<sub>3</sub> vegetation. It has been argued, however, that 12-34% (mean=20%) of C<sub>4</sub> biomass persisted through most of the Miocene before the C<sub>4</sub> expansion (Fox and Koch 2004) based on  $\delta^{13}\text{C}$  values in soil carbonates. As a result, an upper limit of C<sub>3</sub> consumption was calculated using drought-stressed C<sub>3</sub> vegetation reported from Kenya by Passey and others (2002). This water-deprived habitat sits at the uppermost range of C<sub>3</sub> vegetation with a mean value of  $\delta^{13}\text{C} = -24.6 \pm 1.1\text{‰}$  (95% confidence). After model adjustments, the upper boundary for an ungulate consuming water-stressed C<sub>3</sub> vegetation was  $-6.4\text{‰}$ . Therefore, an individual Barstovian mammal must have a  $\delta^{13}\text{C}$  value above  $-6.4\text{‰}$  to have been unquestionably consuming C<sub>4</sub> vegetation.

Similarly, a lower boundary was estimated for water-stressed C<sub>3</sub> environments undergoing drought. Using the same drought-stressed C<sub>3</sub> vegetation from Kenya (Passey *et al.* 2002), the lower limit of a water-stressed C<sub>3</sub> biome was  $-8.7\text{‰}$ . It is possible that values above this range reflect a C<sub>4</sub> vegetation component up to 15-20% of the bulk diet, so this  $\delta^{13}\text{C}$  value represents the lower limit of water-stressed C<sub>3</sub> vegetation or possible C<sub>4</sub> component. Values of  $\delta^{13}\text{C}$  below this are indicative of a pure C<sub>3</sub> diet. As aridity in environments reflects a gradient, faunal values approaching this limit can still indicate vegetation consumption in arid conditions.



## 4. RESULTS

Table 2 presents summary statistics and mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for genera in each local fauna, combined groups, and total local faunas.

### 4.1 Faunal Results

Faunal averages with more than one sample within localities were compared using ANOVA statistical tests. P-values between pairs are reported in Table 3. Due to small and uneven sample sizes, I relied on the Tukey-Kramer HSD post hoc test to predict probabilities of significant differences between means, however, results are also reported using the Fisher LSD post hoc test. Statistically insignificant pairs were combined to increase sample size and reduce error around mean values; these are referred to as “combined groups.” P-values between combined groups are reported in Table 4. Genera with only one representative sample were left out of the statistical tests and were only discussed if they crossed a significant boundary in the model.

#### 4.1.1 Hottell Ranch/ Immense Journey Local Fauna (HI)

No significant differences were found among mean  $\delta^{13}\text{C}$  values (Table 3). There are, however, several significantly different mean  $\delta^{18}\text{O}$  values. The leptomerycid *Pseudoparablastomeryx* ( $\delta^{18}\text{O}=22.5\%$ ) has significantly lower  $\delta^{18}\text{O}$  values than the “browsing” horse *Parahippus* ( $\delta^{18}\text{O}=25.9\%$ ,  $p<0.028$ ). The dromomerycid *Rakomeryx* ( $\delta^{18}\text{O}=26.8\%$ ) has significantly higher  $\delta^{18}\text{O}$  values than both the rhinoceros *Peraceras* ( $\delta^{18}\text{O}=23.5\%$ ,  $p<0.002$ ) and *Pseudoparablastomeryx* ( $\delta^{18}\text{O}=22.5\%$ ,  $p<0.025$ ). The combined group of perissodactyls (Table 4), which includes *Peraceras*, *Teleoceras*, *Tapiravus*, *Hypohippus*, *Parahippus*, *Merychippus*, and *Neohipparion*, is not significantly different from *Merycodus*.

#### 4.1.2 Norden Bridge Local Fauna (NB)

The “grazing” horse *Neohipparion* ( $\delta^{13}\text{C} = -8.0\%$ ) has a significantly higher mean  $\delta^{13}\text{C}$  value than the other common horse *Merychippus* ( $\delta^{13}\text{C} = -9.9\%$ ,  $p < 0.010$ ), the less common, smaller “grazing” horse *Calippus* ( $\delta^{13}\text{C} = -9.9\%$ ,  $p < 0.007$ ), and the dromomerycid *Bouromeryx* ( $\delta^{13}\text{C} = -9.9\%$ ,  $p < 0.001$ , Table 3). The combined group of equids (Table 4) includes *Megahippus*, *Merychippus*, *Calippus*, and *Protohippus* and is not significantly different from the combined group of artiodactyls, which include *Ticholeptus* and *Bouromeryx*. There are no significant differences in mean  $\delta^{18}\text{O}$  values between any of the groups tested.

#### 4.1.3 Valentine Quarry Local Fauna (VQ)

Several genera stand out in this local fauna (Table 3). The oreodont *Ustatochoerus* yields a mean  $\delta^{13}\text{C}$  value ( $\delta^{13}\text{C} = -11.3\%$ ) significantly lower than *Merychippus* ( $\delta^{13}\text{C} = -9.0\%$ ,  $p < 0.024$ ), *Calippus* ( $\delta^{13}\text{C} = -9.0\%$ ,  $p < 0.012$ ), *Protohippus* ( $\delta^{13}\text{C} = -8.8\%$ ,  $p < 0.002$ ), and *Pliohippus* ( $\delta^{13}\text{C} = -9.1\%$ ,  $p < 0.015$ ). All other significant differences occur between mean  $\delta^{18}\text{O}$  values. The “browsing” horse *Parahippus* yields  $\delta^{18}\text{O}$  values ( $\delta^{18}\text{O} = 25.0\%$ ) significantly lower than *Protohippus* ( $\delta^{18}\text{O} = 30.0\%$ ,  $p < 0.000$ ) and the camel *Procamelus* ( $\delta^{18}\text{O} = 28.8\%$ ,  $p < 0.000$ ). Values of  $\delta^{18}\text{O}$  in *Protohippus* ( $\delta^{18}\text{O} = 30.0\%$ ) are also significantly higher than the rhinoceros *Peraceras* ( $\delta^{18}\text{O} = 26.0\%$ ,  $p < 0.012$ ). The peccary *Dyseohyus* ( $\delta^{18}\text{O} = 24.6\%$ ) has a mean  $\delta^{18}\text{O}$  value lower than *Merychippus* ( $\delta^{18}\text{O} = 27.8\%$ ,  $p < 0.039$ ), *Protohippus* ( $\delta^{18}\text{O} = 30.0\%$ ,  $p < 0.003$ ), and *Procamelus* ( $\delta^{18}\text{O} = 28.8\%$ ,  $p < 0.007$ ). The combined group of perissodactyls (Table 4) includes *Peraceras*, *Merychippus*, *Calippus*, and *Pliohippus*.

#### 4.1.4 *C<sub>4</sub> consumption*

One specimen is above the upper limit of water-stressed  $C_3$  vegetation consumption ( $\delta^{13}C = -6.4\%$ ) and indicates unequivocal  $C_4$  consumption (HI *Neohipparion*  $\delta^{13}C = -6.0\%$ ). It is important to note, however, that no faunal averages approach this limit nor plot in the range for  $C_3$  water-stressed vegetation.

#### 4.2 *Local Results*

When taken as a whole, there are no significant differences in mean  $\delta^{13}C$  values among the local faunas (Table 5). The Hottell/Immense, Norden Bridge, and Valentine Quarry local faunas all plot in the open canopy range below the limit for drought-stressed  $C_3$  or possible  $C_4$  component ( $\delta^{13}C = -9.1 \pm 0.3\%$ ,  $-9.3 \pm 0.4\%$ ,  $-8.9 \pm 0.3\%$  respectively).

With regard to mean  $\delta^{18}O$  values, the HI local fauna ( $\delta^{18}O = -24.8 \pm 0.5\%$ ) is significantly lower than the NB or VQ local faunas ( $\delta^{18}O = 26.8 \pm 0.6\%$ ,  $27.0 \pm 0.7\%$  respectively).

## 5. DISCUSSION

### 5.1 Significance within local faunas

#### 5.1.1 Hottell Ranch/ Immense Journey local fauna

All individuals from the HI local fauna yield  $\delta^{13}\text{C}$  values in the open canopy range (Fig. 3). Eleven individuals fall into the water-stressed  $\text{C}_3$  or possible  $\text{C}_4$  component range and one individual yields unequivocal  $\text{C}_4$  consumption (to be discussed in section 5.2). However, there were no significant differences between the mean faunal values in carbon (Table 3, 4), and all faunal averages plot in the upper ranges of an open  $\text{C}_3$  canopy (Fig. 4, 7). This indicates homogeneity in the biome. Of the genera sampled, 8 of the 13 genera are brachydont and interpreted as browsers (Janis *et al.* 2004). Despite the openness of the biome, most of its biomass must have been browse and may be analogous to a woodland savanna, which may include wooded  $\text{C}_3$  savannas, shrub-lands, or woodlands.

*Pseudoparablastomeryx*, a small leptomerycid, yielded a significantly lower mean  $\delta^{18}\text{O}$  value ( $\delta^{18}\text{O}=22.5\pm0.6\%$ ) than the combined group of perissodactyls ( $\delta^{18}\text{O}=24.8\pm0.5\%$ , *Peraceras*, *Teleoceras*, *Tapiravus*, *Hypohippus*, *Parahippus*, *Merychippus*, and *Neohipparion*, Fig. 7). *Pseudoparablastomeryx* is commonly interpreted to be a browser due to its brachydont teeth (Janis *et al.* 2004). Its low  $\delta^{18}\text{O}$  values could show preference for wetter habitats with, but its  $\delta^{13}\text{C}$  values do not approach the boundary for wet, closed biomes. Additionally, postcranial analysis reveals fused metapodials (Janis and Theodor 2014), a common adaptation for cursoriality and living in open habitats. This suggests *Pseudoparablastomeryx* was instead an evaporation insensitive, obligate drinker.

*Rakomeryx*, a medium-sized dromomerycid, yielded a significantly higher mean  $\delta^{18}\text{O}$  value ( $\delta^{18}\text{O}=26.8\pm2.1\%$ ) than the combined group of perissodactyls (Fig. 7). Brachydont teeth (Janis *et al.* 2004) and fine microwear with few scratches (Semprebon *et al.* 2004) suggest *Rakomeryx* was a committed browser. The high  $\delta^{18}\text{O}$  values may indicate that *Rakomeryx* consumed most of its browse in dry areas or was evaporation sensitive and relied partly on leaf-water. Since *Rakomeryx* does not have significantly higher  $\delta^{13}\text{C}$  values than other members of the fauna, it was likely evaporation sensitive.

#### 5.1.2 Norden Bridge local fauna

All individuals from the NB local fauna yield  $\delta^{13}\text{C}$  values in the open canopy range (Fig. 3). Eleven individuals plot in the water-stressed  $\text{C}_3$  or possible  $\text{C}_4$  component range. No individual yields a value consistent with  $\text{C}_4$  consumption or consumption of  $\text{C}_3$  in a closed habitat.

*Neohipparion*, a common, three-toed horse, yielded a significantly higher mean  $\delta^{13}\text{C}$  value ( $\delta^{13}\text{C}= -8.0\pm0.7\%$ , Table 4) than the combined group of equids ( $\delta^{13}\text{C}= -9.6\pm0.5\%$ , *Megahippus*, *Merychippus*, *Calippus*, and *Protohippus*) and the combined group of artiodactyls ( $\delta^{13}\text{C}= -9.9\pm0.5\%$ , *Ticholeptus* and *Bouromeryx*). *Neohipparion* has been widely interpreted as a grazer from hypsodonty indices (Janis *et al.* 2004) and mesowear and microwear studies (MacFadden *et al.* 1999; Fraser and Theodor 2013). Previous isotope studies also interpret *Neohipparion* as grazing in open areas (MacFadden and Cerling 1996; MacFadden *et al.* 1999; Kita *et al.* 2014) and incorporating  $\text{C}_4$  vegetation during the  $\text{C}_4$  grassland expansion. The significantly higher mean  $\delta^{13}\text{C}$  value of *Neohipparion* in the Barstovian is also consistent with a grazing niche, presumably consuming mostly  $\text{C}_3$  grasses.

All taxon averages plot in the upper open C<sub>3</sub> canopy range (Fig. 5, 8), but seven of the eleven genera sampled are brachydont (Janis *et al.* 2004) and have been interpreted as browsers. Again, much of the biomass of this open biome must have been browse, but the significant mean of *Neohipparion* suggest definite patches of C<sub>3</sub> grass. The NB local fauna likely represents a biome analogous to a woodland savanna.

#### 5.1.3 Valentine Quarry local fauna

All individuals and faunal averages from the VQ local fauna yield  $\delta^{13}\text{C}$  values in the open canopy range (Figs. 3,6,9). Eleven individuals plot in the water-stressed C<sub>3</sub> or possible C<sub>4</sub> component range with no individuals yielding unequivocal C<sub>4</sub> consumption or consumption of vegetation in a closed habitat.

*Ustatochoerus*, a large oreodont, yielded a mean  $\delta^{13}\text{C}$  value ( $\delta^{13}\text{C} = -11.3 \pm 1.7\%$ ) significantly lower than that of the combined group of perissodactyls ( $\delta^{13}\text{C} = -9.1 \pm 0.4\%$ , *Peraceras*, *Merychippus*, *Calippus*, and *Plihippus*, Table 4). With mesodont teeth (Stevens and Stevens 1998), *Ustatochoerus* may have been a mixed feeder. Significantly lower  $\delta^{13}\text{C}$  values suggest that it preferred wetter, denser habitats than the combined group of perissodactyls (Fig. 9), primarily horses; however, neither individual or faunal mean values plot in the closed canopy biome. Instead, the presence of this significantly lower mean  $\delta^{13}\text{C}$  value may be indicative of a habitat within the otherwise open biome analogous to the Riparian Thicket (Fig. 2, Codron *et al.* 2005), which grew fairly dense vegetation in an open Kenyan savanna.

Several genera had significantly different mean  $\delta^{18}\text{O}$  values from the rest of the local fauna. *Parahippus* ( $\delta^{18}\text{O} = 25.0 \pm 0.5\%$ ) had a significantly lower mean value than *Procamelus* ( $\delta^{18}\text{O} = 28.8 \pm 1.0\%$ , Tables 3, 4). This may indicate that *Parahippus*, a sub-

mesodont horse interpreted as a browser (Janis *et al.* 2004), had a different hydration strategy than *Procamelus*. It is plausible that *Procamelus* was more evaporation sensitive than *Parahippus*, and may have been somewhat drought tolerant.

*Protohippus* yielded a significantly higher mean  $\delta^{18}\text{O}$  value ( $\delta^{18}\text{O}=30.0\pm1.7\%$ ) than *Parahippus* ( $\delta^{18}\text{O}=25.0\pm0.5\%$ ) and the combined group of perissodactyls ( $\delta^{18}\text{O}=27.1\pm0.7\%$ , Tables 3, 4). Previous studies found that *Protohippus*, a large three-toed horse, was a grazer based on its high hypsodonty index (Janis *et al.* 2004) and on dental mesowear and microwear (Fraser and Theodor 2013). The high mean  $\delta^{18}\text{O}$  values, coupled with previous interpretations, suggest that *Protohippus* consumed grasses in open, dry habitats where leaf-water  $\delta^{18}\text{O}$  values would be elevated from water stress.

*Dyseohyus*, a small peccary, yielded a significantly lower mean  $\delta^{18}\text{O}$  value ( $\delta^{18}\text{O}=24.6\pm2.3\%$ ) than the combined group of perissodactyls (Table 4). The low mean value may indicate it was living in a wetter habitat or was evaporation insensitive.

Of the local faunas sampled, the VQ local fauna has the greatest number of significantly different pairs. This suggests that the environment was less homogeneous than the other local faunas even though its mean faunal carbon value is not significantly different than the other local faunas (Table 5). With *Protohippus* consuming vegetation in open, grassy areas and *Ustatochoerus* and *Dyseohyus* consuming vegetation in wetter, more densely vegetated areas, there were more distinct habitats present in the biome represented by the VQ local fauna. Only seven of the fifteen genera sampled were brachydont (Janis *et al.* 2004) and were presumably consuming browse, but this local fauna indicates the presence of the most varied habitats. The range of mean values yielded by the faunas (Figs. 6, 9) indicates a riparian thicket-like habitat surrounding a

river grading out to a woodland savanna with grassy habitats. This is supported by the Kilgore Flora, a temporally equivalent macroflora found near the Valentine Quarry localities. MacGinitie (1962) concluded that the Kilgore Flora was taphonomically biased towards streamside plants leaving an overabundance of riparian fossils. Small amounts of grass and shrub pollen and seeds indicate the presence of savanna-like habitats on the floodplain further from the depositional channel (MacGinitie 1962). The collection of megaflorea and microflora suggest a riparian thicket habitat grading into a grassy, mixed oak and pine woodland (MacGinitie 1962). The stable carbon and oxygen isotopes from the local fauna are consistent with this interpretation.

## 5.2 *C<sub>4</sub> vegetation in middle Miocene Nebraska*

One individual indicates unequivocal C<sub>4</sub> consumption (HI *Neohipparion*  $\delta^{13}\text{C} = -6.0\%$ ). This appears to be the earliest record of C<sub>4</sub> consumption in a mammal in the Great Plains, followed by probably C<sub>4</sub> consumption by the equid *Cormohipparion* from Ashfall Fossil Beds ( $\delta^{13}\text{C}$  up to  $-4\%$ , Clementz *et al.* 2001). In the upper member of the Barstow Formation of California (14.0-13.4Mya), the individual equids *Scaphohippus* ( $\delta^{13}\text{C} = -6.3\%$ ) and *Acritohippus* ( $\delta^{13}\text{C} = -6.2\%$ ) also yielded values high enough to indicate unequivocal C<sub>4</sub> consumption (Feranec and Pagnac 2013) inferred by the model used in this study. A study of paleosol carbonates suggests the 12-34% (mean=20%) of biomass was employing C<sub>4</sub> photosynthesis in the early and middle Miocene (Fox and Koch 2004). Most faunal isotope studies suggest that herbivores were not consuming C<sub>4</sub> vegetation if it was indeed present (Passey *et al.* 2002; Secord *et al.* 2008; Boardman and Secord 2013; Kita *et al.* 2014), but phylogenetic studies of foliar anatomy and nuclear and chloroplast genes also suggest C<sub>4</sub> vegetation had much earlier origins and was present in small



patches up until C<sub>4</sub> grassland expansion during the later Neogene (Christin *et al.* 2008; Vicentini *et al.* 2008). If C<sub>4</sub> vegetation was present as mean 20% of biomass, it is possible that vegetation models employed are calibrated too low to detect C<sub>4</sub> consumption or that mammalian herbivores did not exploit it as a food resource.

Individuals with  $\delta^{13}\text{C}$  values plotting in the range water-stressed C<sub>3</sub> vegetation may have alternatively been consuming up to 15-20% C<sub>4</sub> vegetation. Out of all 126 bulk enamel samples, 34 individuals (27% of the total sample) yielded values in this range. If I assume that all individuals plotting in the water-stressed range were actually consuming 20% C<sub>4</sub> vegetation, C<sub>4</sub> vegetation would only comprise ~5% of total consumed biomass.

This calculation indicates that very few mammals were exploiting C<sub>4</sub> vegetation present in the biome, or that the amount of available C<sub>4</sub> is overestimated. This finding is similar to that of an earlier study of Clarendonian and Hemphillian faunas that also found little evidence for C<sub>4</sub> consumption, although mammals in the C<sub>3</sub> water-stressed range could conceivably have been consuming small amounts of C<sub>4</sub> vegetation (Kita *et al.* 2014).

### 5.3 Barstovian biomes in Nebraska

Comparison of whole faunas reveals no significant difference between mean  $\delta^{13}\text{C}$  values (Table 5). All local faunas have mean  $\delta^{13}\text{C}$  values that plot in the upper ranges of open canopy C<sub>3</sub> biomes (Fig. 2). All individuals were consuming vegetation grown under an open canopy with some water-stressed vegetation, or the presence small amounts of C<sub>4</sub> (Fig. 3). While one individual does show unequivocal C<sub>4</sub> consumption, the data do not support the hypothesis that any more than ~5% of total biomass was utilizing C<sub>4</sub> photosynthesis. The homogeneity of the data suggests that Nebraska's biomes during the

Barstovian were characterized by open woodland-savannas. Small habitats of riparian thicket-like areas and open C<sub>3</sub> grassy areas may also have existed.

One irregularity that occurs in  $\delta^{13}\text{C}$  values is the very positive values yielded by *Tapiravus* from each local fauna. Modern tapirs live in densely forested habitats and, through the evolutionary history of tapirs, the form and function of a tapir has remained relatively unchanged (DeSantis and MacFadden 2007). Fossil tapirs yield consistent  $\delta^{13}\text{C}$  values (range -10.1‰ to -14.3‰) and have been used as indicators of densely forested habitats (DeSantis and MacFadden 2007). The *Tapiravus* individuals from this study all plot between  $\delta^{13}\text{C} = -10.3\text{‰}$  and  $\delta^{13}\text{C} = -9.0\text{‰}$ . It is likely that these tapirs were consuming vegetation in more riparian habitats, but that the Barstovian biomes were homogeneously open and could not register very negative  $\delta^{13}\text{C}$  values.

The HI local fauna yields a significantly lower mean  $\delta^{18}\text{O}$  value than the NB or VQ local faunas. Differences in whole faunal  $\delta^{18}\text{O}$  values are unlikely to be due to physiological differences in the taxa sampled as each local fauna consisted of a diversity of ungulates. Local differences are more likely to be caused by waters sources from different watersheds. The HI local fauna is separated geographically from the NB and VQ local faunas, although the NB and HI local faunas are both contained within the Cornell Dam Member of the Valentine Formation. It has been noted that the fossiliferous bed at the HI localities contained locally sourced gravel instead of igneous and metamorphic gravel from Rocky Mountain basement uplifts of the Laramide Orogeny (Voorhies *et al.* 1987). This suggests a river disconnected from the drainage basins near the Rocky Mountains may supplied much of the sediment to this locality. A differing water source may account for the HI local fauna's lower mean  $\delta^{18}\text{O}$  value.

#### 5.4 Biome change from the Barstovian to the Clarendonian (~10Mya)

After the middle Miocene (12-8 Mya), browser diversity began to decline, presumably due to a decline in the amount of available browse and, eventually, the expansion of C<sub>4</sub> grasslands (Janis *et al.* 2004). To examine if this decline of the middle Miocene browsing diversity is detectable as a change in biomes, Barstovian faunal data are compared to two previously sampled Clarendonian local faunas from Nebraska. The North Shore and Pratt Slide local faunas, assigned to the late Clarendonian (10.0-9.0 Mya, Tedford *et al.* 2004), were compared as wholes to the local faunas in this study. P-values between pairs of local faunas are reported in Table 6.

The Pratt Slide faunal values showed a significantly lower local mean  $\delta^{13}\text{C}$  value ( $\delta^{13}\text{C} = -11.8 \pm 0.4\%$ ) than all Barstovian local faunas. This is not surprising as Kita and others (2014) found that Pratt Slide was also significantly lower than the other pre-C<sub>4</sub> grassland expansion local faunas sampled. Although it is possible that densely vegetated biomes existed during the Clarendonian, Pratt Slide data likely represents a habitat in an incised valley (Voorhies, pers. comm.) rather than the channel deposits represented by the North Shore, Hottell Ranch/ Immense Journey, Norden Bridge, and Valentine Quarry local faunas.

The mean  $\delta^{13}\text{C}$  value of the North Shore local fauna ( $\delta^{13}\text{C} = -9.4 \pm 0.4\%$ ), however, showed no significant differences from any Barstovian local fauna (Fig. 10). This suggests that both Barstovian and Clarendonian biomes were homogeneously open. Kita and others (2014) interpreted the North Shore local fauna as analogous to a “dry” woodland-savanna or C<sub>3</sub> grassland. The predictive model is limited, however, as it cannot distinguish between endmembers of the woodland-savanna gradient because they possess

the same degree of openness. It is possible that, while browser diversity decline from the Barstovian to the Clarendonian is not marked by a significant change in biome, a subtler change in vegetation occurred to spark the decline in browser diversity that is undetectable by the data.

## 6. CONCLUSIONS

The goal of this study was to construct a model for inferring middle Miocene terrestrial biomes using stable carbon isotopes in mammal teeth and to address whether middle Miocene biomes in Nebraska, were open savanna-like environments, as inferred from some other studies, more forested closed environments, or a mixture of both. Ungulates living in the central Great Plains during the middle Miocene consumed predominantly  $C_3$  vegetation. One individual *Neohipparion* shows definitive  $C_4$  consumption before the expansion of  $C_4$  grasses, and represents one of the earliest examples of a mammal consuming  $C_4$  vegetation. Several other individual mammals show consumption of water-stressed  $C_3$  or a small component of  $C_4$  in a mostly  $C_3$  diet indicating up to 5% of biomass consumed by the fauna could have been  $C_4$  vegetation. The middle Miocene (Barstovian) biomes were characterized by predominantly open biomes, such as woodland, bushland, or wooded savanna. Certain taxa indicate the presence of smaller habitats within the open biome such as grassy patches and riparian thickets. These findings are broadly consistent with earlier interpretations. The peak in browser diversity in the middle Miocene did not correspond with the partitioning of browsers in heavily forested areas. The large diversity of browsers in the Barstovian must have subsisted on browse growing in open habitats and partitioned resources in a manner undetectable by the methods in this study. There was no detectable change in the biome between the Barstovian and the younger Clarendonian as browser diversity began to decline, but subtler changes in vegetation within the biome are not detectable by the model and do not preclude the possibility of changes in vegetation, such as an increase in  $C_3$  grasses.

## 7. REFERENCES

- Axelrod, D.I. 1985. Rise of the Grassland Biome, Central North America. *Botanical Review*. 51(2): 163-201.
- Balasse, M. 2001. Detection of dietary changes by intra-tooth carbon and nitrogen isotopic analysis: An experimental study of dentine collagen of cattle (*Bos taurus*). *Journal of Archaeological Science*. 28: 235-245.
- Balesdent, J., Girardin, C., Mariotti, A. 1993. Site-related  $^{13}\text{C}$  of tree leaves and soil organic matter in a temperate forest. *Ecology*. 74(6):1713-1721.
- Boardman, G.S. and Secord, R. 2013. Stable isotope paleoecology of White River ungulates during the Eocene-Oligocene climate transition in northwestern Nebraska. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 375: 38-49.
- Bryant, J.D. and Froelich, P.N. 1995. A model of oxygen isotope fractionation in body water of large mammals. *Geochimica et Cosmochimica Acta*. 59(21): 4523-4537.
- Cerling, T.E. and 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., 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., Hart, J.A., Hart, T.B., 2004. Stable isotope ecology in the Ituri Forest. *Oecologia*. 138: 5–12.
- Cerling, T.E., Wang, Y., Quade, J. 1993. Expansion of  $\text{C}_4$  ecosystems as an indicator of global ecological change in the late Miocene. *Nature*. 361: 344-345.

- Christin, P.A., Besnard, G., Samaritani, E., Duvall, M.R., Hodkinson, T.R., Savolainen, V., Salamin, N. 2008. Oligocene CO<sub>2</sub> Decline Promoted C<sub>4</sub> photosynthesis in grasses. *Current Biology*. 18: 37-43.
- Clementz, M.T., Holroyd, P.A., Koch, P.L. 2008. Identifying aquatic habits of herbivorous mammals through stable isotope analysis. *Palaaios*. 23: 574-585.
- Codron, J., Codron, D., Lee-Thorp, J.A., Sponheimer, M., Bond, W.J., de Ruiter, 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. and Schoch, R.M. Tapiroidea and other moropomorphs. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.). *Evolution of Tertiary mammals of North America: Volume 1, terrestrial carnivores, ungulates, and ungulate like mammals*. Cambridge University Press, Cambridge.
- Coombs, M.C. 1998. Chalicotherioidea. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.). *Evolution of Tertiary mammals of North America: Volume 1, terrestrial carnivores, ungulates, and ungulate like mammals*. Cambridge University Press, Cambridge.
- Corner, R.G. 1976. An early Valentinian vertebrate local fauna from southern Webster Country, Nebraska. M.S. Thesis, University of Nebraska, Lincoln.
- DeNiro, M.J. and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*. 42: 495-506.

DeSantis, L.R.G. and MacFadden, B.J. 2007. Identifying forested environments in Deep Time using fossil tapirs: Evidence from evolutionary morphology and stable isotopes. *Courier Forschungsinstitut Senckenberg*. 258: 147-157.

Douwe J.J. van Hinsbergen, Lennart V. de Groot, Sebastiaan J. van Schaik, Wim Spakman, Peter K. Bijl, Appy Sluijs, Cor G. Langereis, and Henk Brinkhuis: A Paleolatitude Calculator for Paleoclimate Studies (model version 2.1), *PLOS ONE*, 2015.

Edwards, E.J., Osborne, C.P., Strömberg, C.A.E., Smith, S.A., C<sub>4</sub> Grasses Consortium. 2010. The origins of C<sub>4</sub> grasslands: Integrating evolutionary and ecosystem science. *Science*. 328(5978): 587-591.

Ehleringer, J.R., Field, C.B., Lin, Z.F., Kuo, C.Y. 1986. Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline. *Oecologia*. 70: 520-526.

Ehleringer, J.R., Lin, Z.F., Field, C.B., Sun, G.C., Kuo, C.Y. 1987. Leaf carbon isotope ratios of plants from a subtropical monsoon forest. *Oecologia*. 72(1): 109-114.

Ehleringer, J.R., Sage, R.F., Flanagan, L.B., Pearcy, R.W., 1991. Climate change and the evolution of C<sub>4</sub> photosynthesis. *Trends in Ecology and Evolution*. 6: 95–99.

Feranec, R.S. and MacFadden, B.J., 2006. Isotopic discrimination of resource partitioning among ungulates in C<sub>3</sub>-dominated communities from the Miocene of Florida and California. *Paleobiology*. 32: 191–205

Feranec, R.S. and Pagnac, D. 2013. Stable carbon isotope evidence for the abundance of C<sub>4</sub> plants in the middle Miocene of southern California. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 388: 42-47.



- Fox, D.L. and Koch, P.L. 2003. Tertiary History of C<sub>4</sub> Biomass in the Great Plains, USA. *Geol.*, 31: 809-812.
- Fox, D.L. and Koch, P.L. 2004. Carbon and oxygen isotopic variability in Neogene paleosol carbonates: constraints on the evolution of the C<sub>4</sub>-grasslands of the Great Plains, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 207: 311-335.
- Fraser, D. and Theodor, J.M. 2013. Ungulate diets reveal patterns of grassland evolution in North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 369(1): 409-421.
- Frick, C. 1937. Horned ruminants of North America. *Bulletin of the American Museum of Natural History*. 69.
- Friedli, H., Löffler, H., Oeschger, H., Siegenthaler, U., Stauffer, B. 1986. Ice core record of the <sup>13</sup>C/<sup>12</sup>C ratio of atmospheric CO<sub>2</sub> in the past two centuries. *Nature*. 324: 237-238.
- Gidley, J.W. 1907. Revision of the Miocene and Pliocene Equidae of North America. *American Museum of Natural History*. 23: 865-934.
- Graham, H.V., Patzkowsky, M.E., Wing, S.L., Parker, G.G., Fogel, M.L., Freeman, K.H. 2014. Isotopic characteristics of canopies in simulated leaf assemblages. *Geochimica et Cosmochimica Acta*. 144:82-95.
- Hillson, S. 2005. *Teeth*. Second Edition. Cambridge University Press, Cambridge.
- J.A. and Sullivan, R.M. 1981. A small herpetofauna from the type section of the Valentine Formation (Miocene: Barstovian), Cherry County, Nebraska. *Journal of Paleontology*. 55(1): 138-144.

- Honey, J.G., Harrison, J.A. Prothero, D.R., Stevens, M.S. 1998. Camelidae. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.). *Evolution of Tertiary mammals of North America: Volume 1, terrestrial carnivores, ungulates, and ungulate like mammals*. Cambridge University Press, Cambridge.
- Hulbert, Jr., R.C. and MacFadden, B. 1990. Morphological transformation and cladogenesis at the base of the adaptive radiation of Miocene Hypsodont horses. *American Museum Novitates*. 3000:61.
- Janis, C.M. and Manning E. Antilocapridae. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.). *Evolution of Tertiary mammals of North America: Volume 1, terrestrial carnivores, ungulates, and ungulate like mammals*. Cambridge University Press, Cambridge.
- Janis, C.M. and Manning E. Dromomerycidae. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.). *Evolution of Tertiary mammals of North America: Volume 1, terrestrial carnivores, ungulates, and ungulate like mammals*. Cambridge University Press, Cambridge.
- Janis, C.M. and Theodor, J.M. 2014. Cranial and postcranial morphological data in ruminant phylogenetics. *Zitteliana B*. 32: 15-31.
- Janis, C.M., Damuth, J., Theodor, J.M. 2000. Miocene ungulates and terrestrial primary productivity: Where have all the browsers gone? *Proceedings of the National Academy of Science*. 97(14): 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(1-2): 183-198.

- Janis, C.M., Damuth, J., Theodor, J.M. 2004. The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 207: 371-398.
- Jenkins, S.G., Partridge, S.T., Stephenson, T.R., Farley, S.D., Robbins, C.T. 2001. Nitrogen and carbon isotope fractionation between mothers, neonates, and nursing offspring. *Oecologia*. 129:336-341.
- Jessup, K.E., Barnes, P.W., Boutton, T.W. 2003. Vegetation dynamics in a *Quercus-Juniperus* savanna: An isotopic assessment. *Journal of Vegetation Science*. 14: 841-852.
- Kita, Z.A., Secord, R., Boardman, G.S. 2014. A new stable isotope record of Neogene paleoenvironments and mammalian paleoecologies in the western Great Plains during the expansion of C4 grasslands. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 399: 160-172.
- Koch, P.L. 1998. Isotopic reconstruction of past continental environments. *Annual Review of Earth and Planetary Sciences*. 26: 573-613.
- Koch, P.L. 2007. Isotopic study of the biology of modern and fossil vertebrates. In: Michener, R. and Lajtha, K. (Eds.). *Stable Isotopes in Ecology and Environmental Science*, Second Edition, Blackwell Publishing Ltd, Oxford.
- Koch, P.L., Tuross, N., Fogel, M. 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. *Journal of Archaeological Science*. 24: 417-429.

- Kohn, M.J. 1996. Predicting animal  $\delta^{18}\text{O}$ : Accounting for diet and physiological adaptation. *Geochimica et Cosmochimica Acta*. 60(23): 4811-4829.
- Kohn, M.J., Schoeninger, M.J., Valley, J.W. 1996. Herbivore tooth oxygen isotope compositions: Effects of diet and physiology. *Geochimica et Cosmochimica Acta*. 60(23):3889-3896.
- Körner, C., Farquhar, G.D., Roksandic, Z. 1988. A global survey of carbon isotope discrimination in plants from high altitude. *Oecologia*. 74(4):623-632.
- Körner, C., Farquhar, G.D., Wong, S.C. 1991. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. *Oecologia*. 88:30-40.
- Lee-Thorpe, J.A. and van der Merwe, N.J. 1987. Carbon isotope analysis of fossil bone apatite. *South African Journal of Science*. 83: 712-715.
- 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(30): 11201-11205.
- Macdonald, J.R. 1956. A new Clarendonian mammalian fauna from the Truckee Formation of Western Nevada. *Journal of Vertebrate Paleontology*. 30(1): 186-202.
- MacFadden, B. 1992. Fossil horses: Systematics, paleobiology, and evolution of the family Equidae. Cambridge University Press, Cambridge.
- MacFadden, B. 1998. Equidae. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.). *Evolution of Tertiary mammals of North America: Volume 1, terrestrial carnivores, ungulates, and ungulate like mammals*. Cambridge University Press, Cambridge.

- MacFadden, B.J. 1997. Origin and evolution of the grazing guild in new world terrestrial mammals. *Trends in Ecology and Evolution*. 12(5): 182-187.
- MacFadden, B.J. and Cerling, T.E. 1994. Fossil horses, carbon isotopes, and global change. *Trends in Ecology and Evolution*. 9(12):481-486.
- MacFadden, B.J. and 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(1): 103-115.
- MacFadden, B.J., Solounias, N., Cerling, T.E. 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. *Science*. 283(5403): 824-827.
- MacFadden, B.J. and Higgins, P. 2004. Ancient ecology of 15-million-year-old browsing mammals within C<sub>3</sub> plant communities from Panama. *Oecologia*. 140(1): 169-182.
- MacGinitie, H.D. 1962. The Kilgore flora: A late Miocene flora from northern Nebraska. University of California Publications in Geological Sciences. 35(2): 67-158.
- Matthew, W.D. 1926. The evolution of the horse: A record and its interpretation. *Quarterly Review of Biology*. 1(2): 139-185.
- Mead, A.J. 1999. Aspects of the systematics and paleoecologies of the middle to late Miocene North American rhinoceroses *Peraceras*, *Teleoceras*, and *Aphelops*. Dissertation. University of Nebraska-Lincoln.
- Metais, G. and Vislobokova, I. 2007. Basal Ruminants. In: Prothero, D.R. and Foss, S.E. (Eds.). *The Evolution of Artiodactyls*. Johns Hopkins University Press, Baltimore.

- Mooney, H.A., Bullock, S.H., Ehleringer, J.R. 1989. Carbon isotope ratios of plants of a tropical dry forest in Mexico. *Functional Ecology*. 3(2): 137-142.
- 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.
- Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotope fractionation between diet, breath CO<sub>2</sub>, and bioapatite in different mammals. *Journal of Archaeological Science*. 32: 1459–1470.
- Perkins, M.E. and Nash, B.P. 2002. Explosive silicic volcanism of the Yellowstone hotspot: The ash fall tuff record. *Geological Society of America Bulletin*. 114(3): 367-381.
- Prothero, D.R. 1998. Rhinocerotidae. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.). *Evolution of Tertiary mammals of North America: Volume 1, terrestrial carnivores, ungulates, and ungulate like mammals*. Cambridge University Press, Cambridge.
- Prothero, D.R. 2007. Family Moschidae. In: Prothero, D.R. and Foss, S.E. (Eds.). *The Evolution of Artiodactyls*. Johns Hopkins University Press, Baltimore.
- Prothero, D.R. and Liter, M.R. 2008. Systematics of the Dromomerycines and Aletomerycines (Artiodactyla: Palaeomerycidae) from the Miocene and Pliocene of North America. In: Lucas, S.G., Morgan, G.S., Spielmann, J.A., Prothero, D.R. *Neogene Mammals*. New Mexico Museum of Natural History and Science. 44.

- Quade, J. and Cerling, T.E. 1995. Expansion of C<sub>4</sub> grasses in the late Miocene of northern Pakistan: evidence from stable isotopes in paleosols. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 115: 91-116.
- Quade, J., Cerling, T.E., Andrews, P., Alpagut, B. 1995. Paleodietary reconstruction of Miocene faunas from Pasalar, Turkey using stable carbon and oxygen isotopes of fossil tooth enamel. *Journal of Human Evolution*. 28: 373–384.
- Quinn J.H. 1955. Miocene Equidae of the Texas Coastal Plain. Bureau of Economic Geology, University of Texas at Austin. 5516.
- Retallack, G.J. 1997. Neogene expansion of the North American prairie. *Palaios*. 12: 380-390.
- Retallack, G.J. 2001. Cenozoic expansion of grasslands and climatic cooling. *Journal of Geology*. 109(4): 407-426.
- Rountrey, A.N., Fisher, D.C., Vartanyan, S., Fox, D.L. 2007. Carbon and nitrogen isotope analysis of a juvenile woolly mammoth tusk: Evidence of weaning. *Quaternary International* 169-170: 166-173.
- Sandquist, D.R. and Cordell, S. 2007. Functional diversity of carbon-gain, water-use, and leaf-allocation traits in trees of a threatened lowland dry forest in Hawaii. *American Journal of Botany*. 94(9): 1459-1469.
- Schultz, C.B. and Falkenbach, C.H. 1941. Ticholeptinae: A new subfamily of oreodont. *Bulletin of the American Museum of Natural History*. 79:1-105.
- Schultz, C.B. and Falkenbach, C.H. 1968. The Phylogeny of the Oreodonts: Parts One and Two. *Bulletin of the American Museum of Natural History*. 139:1-498.

- Schulze, E.D., Williams, R.J., Farquhar, Schulze, W., Langridge, J., Miller, J.M., Walker, B.H. 1998. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology* 25(4):413-425.
- Secord, R., Wing, S.L., Chew, A. 2008. Stable isotopes in early Eocene mammals as indicators of forest canopy structure and resource partitioning. *Paleobiology*. 34(2): 282-300.
- Semprebon, G., Janis, C., Solounias, N. 2004. The diets of the Dromomerycidae (Mammalia: Artiodactyla) and their response to Miocene vegetational change. *Journal of Vertebrate Paleontology*. 24(2): 427-444.
- Skinner, M.F. and Johnson, W. 1984. Tertiary Stratigraphy and the Frick Collection of Fossil Vertebrates from North-Central Nebraska. *Bulletin of the American Museum of Natural History*. 178: 238-280.
- Sobrado, M.A. and Ehleringer, J.R. 1997. Leaf carbon isotope ratios from a tropical dry forest in Venezuela. *Flora*. 192: 121-124.
- Stebbins, G.L. Coevolution of grasses and herbivores. *Annals of the Missouri Botanical Garden*. 68(1): 75-86.
- Stevens, M.S. and Stevens, J.B. 2007. Family Merycoidodontidae. In: Prothero, D.R. and Foss, S.E. (Eds.). *The Evolution of Artiodactyls*. Johns Hopkins University Press, Baltimore.
- Stewart, G.R., Turnbull, M.H., Schmidt, S., Erskine, P.D. 1995.  $^{13}\text{C}$  natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. *Australian Journal of Plant Physiology* 22(1):51-55



- Stock, C. 1937. A peccary skull from the Barstow Miocene, California. *Proceedings of the National Academy of Science*. 23: 398-404.
- Strömberg, C.A.E. 2002. The origin and spread of grass-dominated ecosystems in the late Tertiary of North America: preliminary results concerning the evolution of hypsodonty. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 177: 59-75.
- Strömberg, C.A.E. 2004. Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North American during the late Eocene to early Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 207(3-4): 239-275.
- Strömberg, 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 Science*. 102(34):11980-11984.
- Strömberg, C.A.E. 2006. Evolution of hypsodonty in equids: testing a hypothesis of adaptation. *Paleobiology*. 32(2): 236-258.
- Strömberg, C.A.E. and McInerney, F.A. 2011. The Neogene transition from C<sub>3</sub> to C<sub>4</sub> grasslands in North America: Assemblage analysis of fossil phytoliths. *Paleobiology*. 37(1): 50-71.
- Swisher, C.C.III. 1992. <sup>40</sup>Ar/<sup>39</sup>Ar dating and its application to the calibration of the North American land-mammal ages. Ph.D. dissertation, University of California, Berkeley.
- Tedford, T.H., Albright III, L.B., Barnosky, A.D., Ferrusquia-Villafranca, I., Hunt Jr., R.M., Storer, J.E., Swisher III, E.E., Voorhies, M.R., Webb, S.D., Whistler, D.P., 2004. Mammalian biochronology of the Arikareean through Hemphillian interval

- (late Oligocene through early Pliocene epochs). In: Woodburne, M.O. (Ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. Columbia University Press, New York, pp. 169–231.
- Tipple, B.J., Meyers, S.R., Pagani, M. 2010. Carbon isotope ratio of Cenozoic CO<sub>2</sub>: a comparative evaluation of available geochemical proxies. *Paleoceanography* 25:PA3202.
- van der Merwe, N.J. 1982. Carbon isotopes, photosynthesis, and archaeology: Different pathways of photosynthesis cause characteristic changes in carbon isotope ratios that make possible the study of prehistoric human diets. *American Scientist*. 233: 976-878.
- van der Merwe, N.J. and Medina, E. 1991. The canopy effect, carbon isotope ratios and food webs in Amazonia. *Journal of Archaeological Science*. 18: 249-259.
- Vincentini, A., Barber, J.C., Aliscioni, S.S., Giussani, L.M., Kellogg, E.A. 2008. The age of the grasses and clusters of origins of C<sub>4</sub> photosynthesis. *Global Change Biology*. 14: 2963-2977.
- Vogel, J.C. 1978. Isotopic Assessment of the dietary habits of ungulates. *South African Journal of Science*. 74(8): 298-301.
- Voorhies, M.R, Holman, J.A., Xiang-Xu, X. 1987. The Hottell Ranch Rhino Quarries (basal Ogallala: medial Barstovian), Banner County, Nebraska. Part 1: Geologic setting, faunal lists, lower vertebrates. *Contributions to Geology, University of Wyoming*. 25(1): 55-69.
- Voorhies, M.R. 1990a. Vertebrate Biostratigraphy of the Ogallala Group in Nebraska. In: Gustavson, T. C. (Ed.). *Geologic Framework and Regional Hydrology: Upper*

- Cenozoic Blackwater Draw and Ogallala Formations, Great Plains. University of Texas Press, Austin. pp. 115-155.
- Voorhies, M.R. 1990b. Vertebrate paleontology of the proposed Norden Bridge Reservoir area, Brown, Cherry, and Keya Paha counties, Nebraska. Technical Report 82-09, Division of Archaeological Research, University of Nebraska, Lincoln.
- Wang, Y. and Cerling, T.E. 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 107: 281-289.
- Wang, Y., Cerling, T.E., MacFadden, B.J. 1994. Fossil horses and carbon isotope: new evidence for Cenozoic dietary, habitat, and ecosystem changes in North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 107: 269-279.
- Waters, N.E. 1980. Some mechanical and physical properties of teeth. In: Vincent, J.F. and Currey, J.D. (Eds.). *The Mechanical Properties of Biological Materials*. Society for Experimental Biology, London.
- Williams, D.G. and Ehleringer, J.R. 1996. Carbon isotope discrimination in three semi-arid woodland species along a monsoon gradient. *Oecologia*. 106: 455-460.
- Webb, S.D. 1998. Hornless Ruminants. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.). *Evolution of Tertiary mammals of North America: Volume 1, terrestrial carnivores, ungulates, and ungulate like mammals*. Cambridge University Press, Cambridge.
- Webb, S.D., 1983. The rise and fall of the Late Miocene ungulate fauna in North America. In: Nitecki, M.N. (Ed.), *Coevolution*. University of Chicago Press, Chicago, IL, pp. 267– 306.

- Woodburne, M.O. 1996. Craniodental analysis of *Merychippus insignis* and *Cormohipparion goorisi* (Mammalia, Equidae), Barstovian, North America. Bulletin of the American Museum of Natural History. 279:397-468
- Yakir, D., DeNiro, M.J., Gat, J.R. 1990. Natural deuterium and oxygen-18 enrichment in leaf water of cotton plants grown under wet and dry conditions: evidence for water compartmentation and its dynamics. Plant, Cell & Environment. 13: 49–56.
- Yan, C., Han, X., Chen, L., Huang, J., Su, B. 1998. Foliar  $\delta^{13}\text{C}$  within temperate deciduous forest: Its spatial change and interspecies variation. Acta Botanica Sinica. 40(9): 853-859.

Figure 1. General geographic distribution of the Nebraskan localities used in this study and their correlated biochronologic (NALMA) and geochronologic (Epoch) age. Local faunas are represented by pie charts displaying the proportions of genera sampled by hypsodonty index. Brachydont genera are shown in black, mesodont genera in grey, and hypsodont genera in white.

Age distributions: Voorhies 1990a and Tedford *et al.* 2004. Hypsodonty indices: Janis *et al.* 2004.

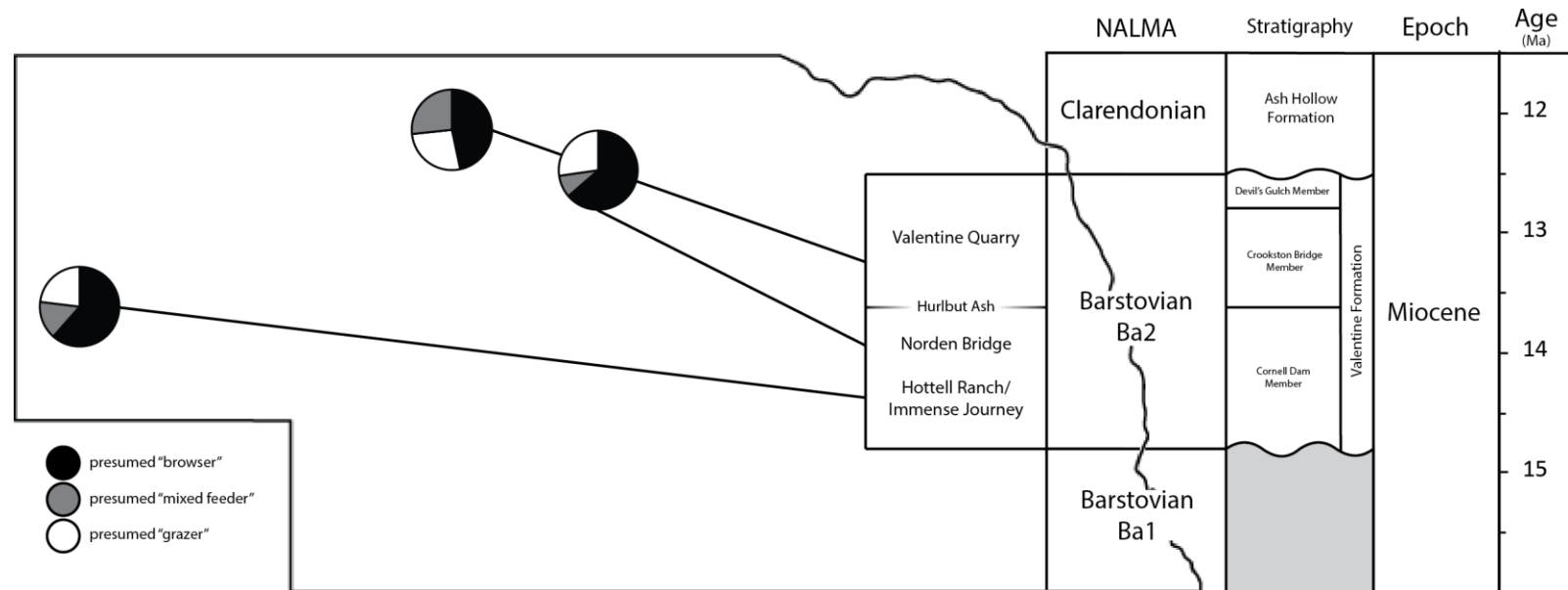


Figure 2. Predictive model for  $\delta^{13}\text{C}$  values of middle Miocene herbivore enamel in various biomes based on  $\delta^{13}\text{C}$  values from modern vegetation normalized to the paleolatitude and altitude of Nebraska, USA with adjustments for diet-to-enamel enrichment and atmospheric changes (see text). Open biomes are shown with circles and closed biomes are squares. Error bars on biomes, habitats within the biomes, and the average  $\delta^{13}\text{C}$  values for the local faunas used in this study represent 95% confidence of the mean ( $1.96 \times \text{S.E.}$ ).

Sources: (A) Cerling, *et al.* 2004, (B) Ehleringer *et al.* 1987, (C) Balesdent *et al.* 1993, (D) Codron *et al.* 2005, (E) Jessup *et al.* 2003, (F) Yan *et al.* 1998, (G) Sobrado and Ehleringer 1997, (H) Mooney *et al.* 1989, (I) Sandquist and Cordell 2007, (J) Williams and Ehleringer 1996, (K) Cerling and Harris 1999, (L) Passey *et al.* 2002

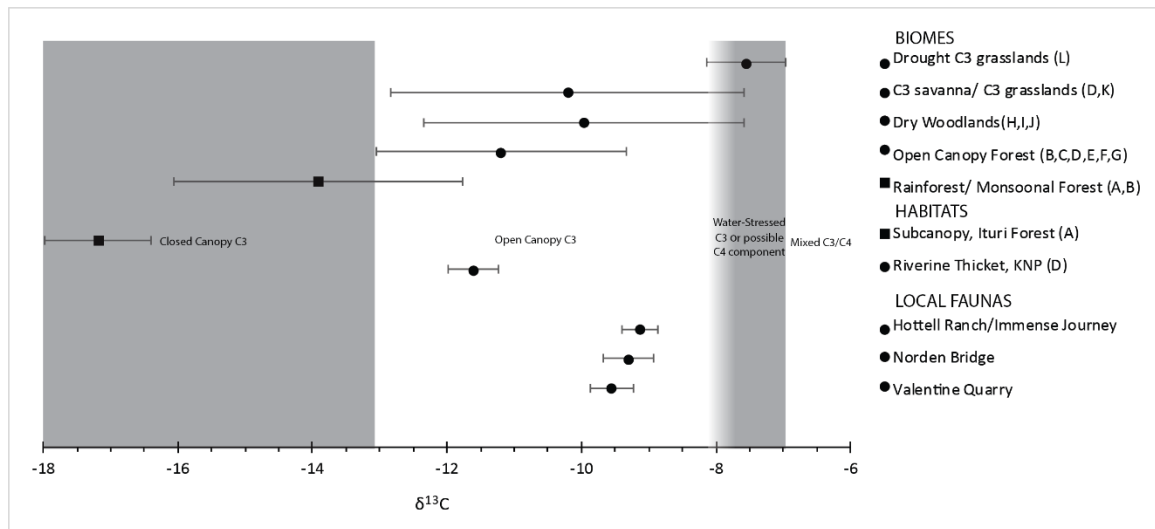


Figure 3. Individual faunal values from the local faunas overlain with the boundaries of the predictive model for  $\delta^{13}\text{C}$  values of herbivore enamel.

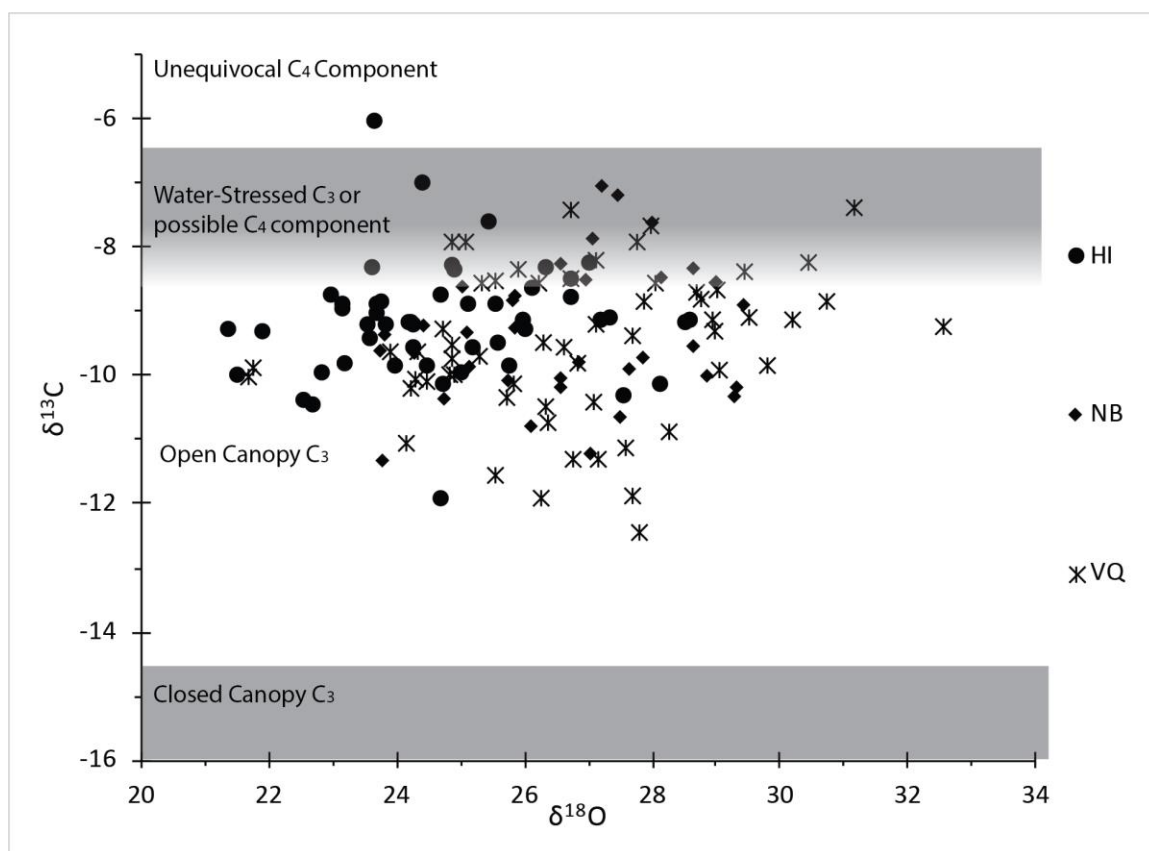


Figure 4. Mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for all genera in Hottell Ranch/Immense Journey with vegetation boundaries. Error on faunal averages represent 95% confidence of the mean of all individuals within that taxa ( $1.96 \times \text{S.E.}$ ).

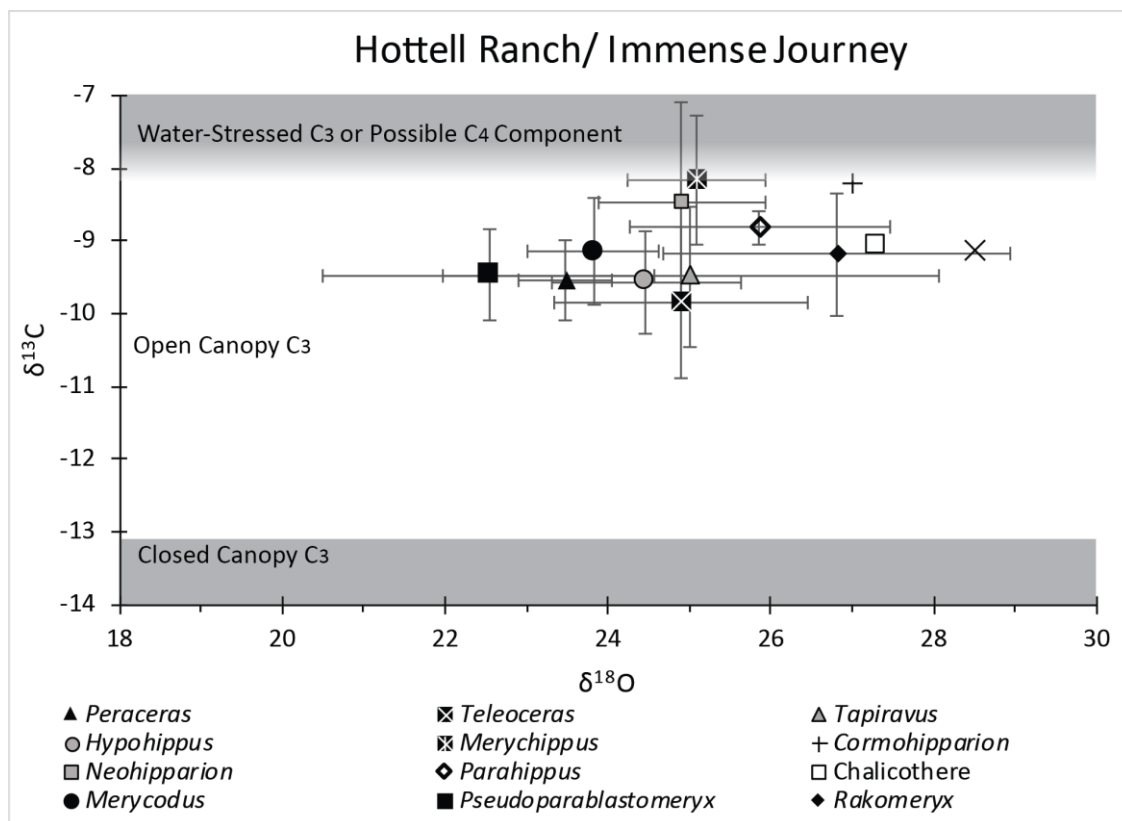




Figure 5. Mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for all genera in Norden Bridge with vegetation boundaries. Error on faunal averages represent 95% confidence of the mean of all individuals within that taxa ( $1.96 \times \text{S.E.}$ ).

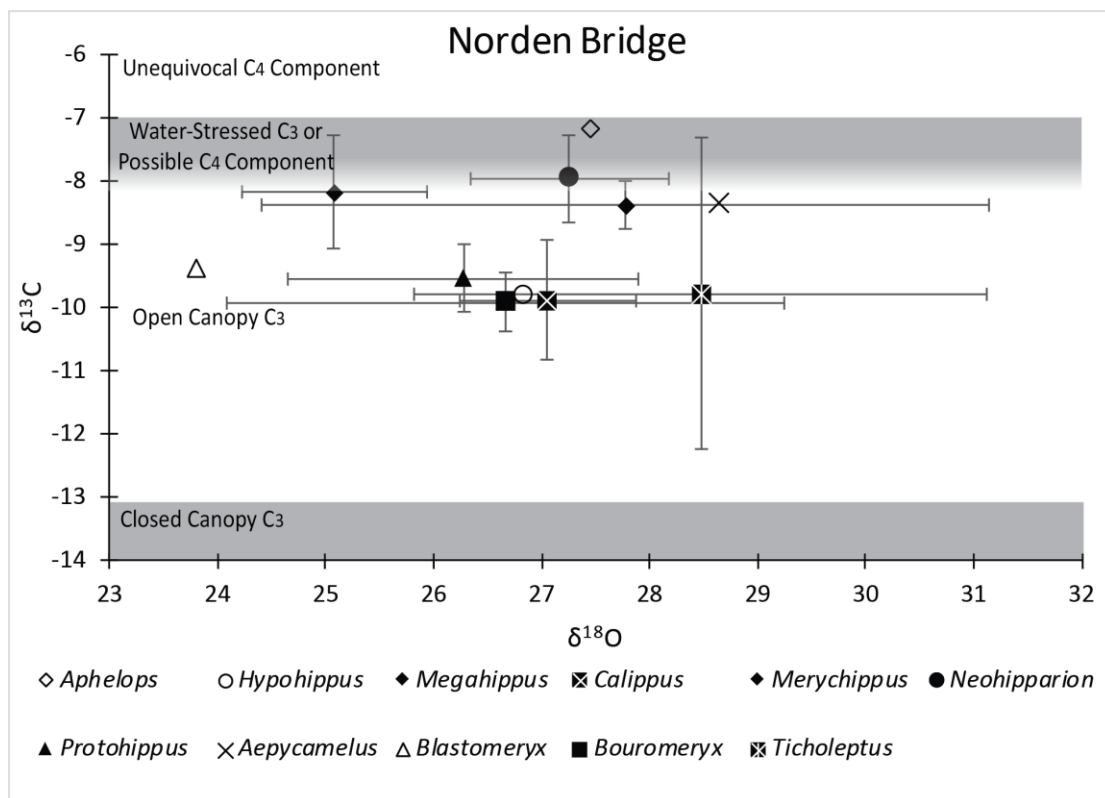


Figure 6. Mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for all genera in Valentine Quarry with vegetation boundaries. Error on faunal averages represent 95% confidence of the mean of all individuals within that taxa ( $1.96 \times \text{S.E.}$ ).

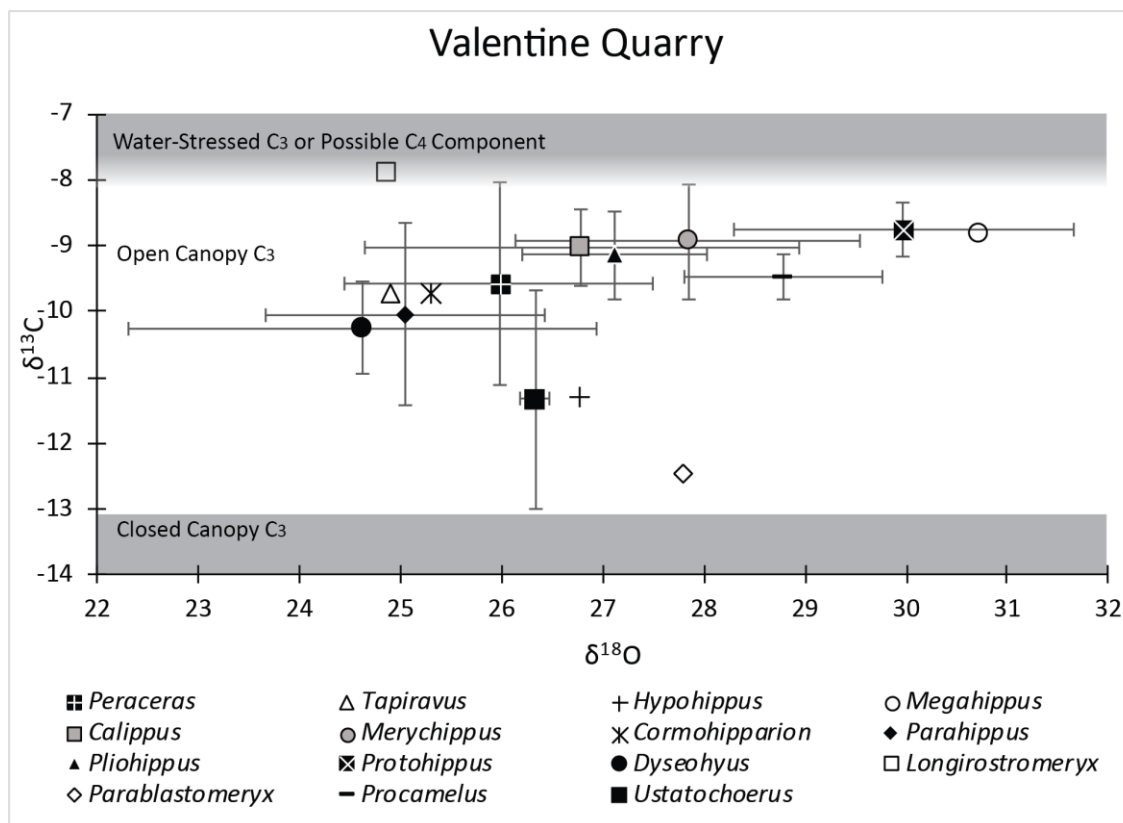


Figure 7. Mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for significant genera and reduced groups in Hottell Ranch/ Immense Journey with vegetation boundaries. Error on faunal averages represent 95% confidence of the mean of all individuals within that taxa ( $1.96 \times \text{S.E.}$ ).

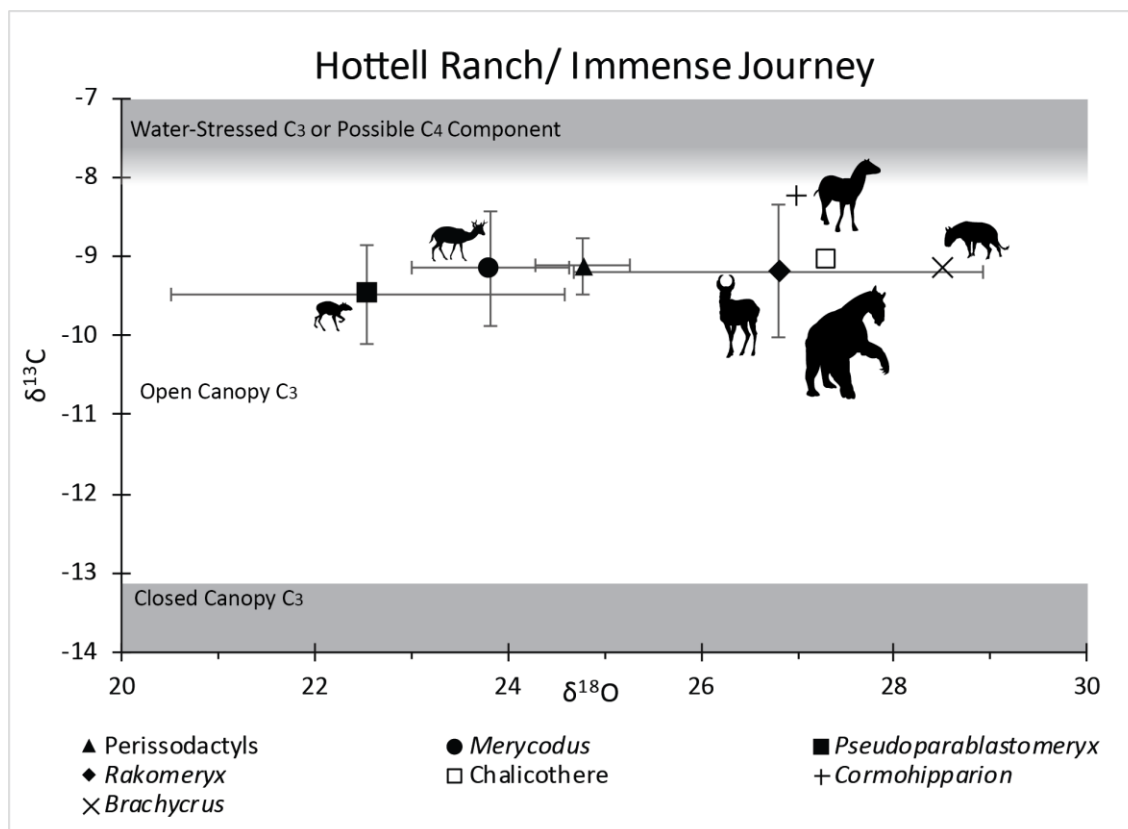


Figure 8. Mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for significant genera and reduced groups in Norden Bridge with vegetation boundaries. Error on faunal averages represent 95% confidence of the mean of all individuals within that taxa ( $1.96 \times \text{S.E.}$ ).

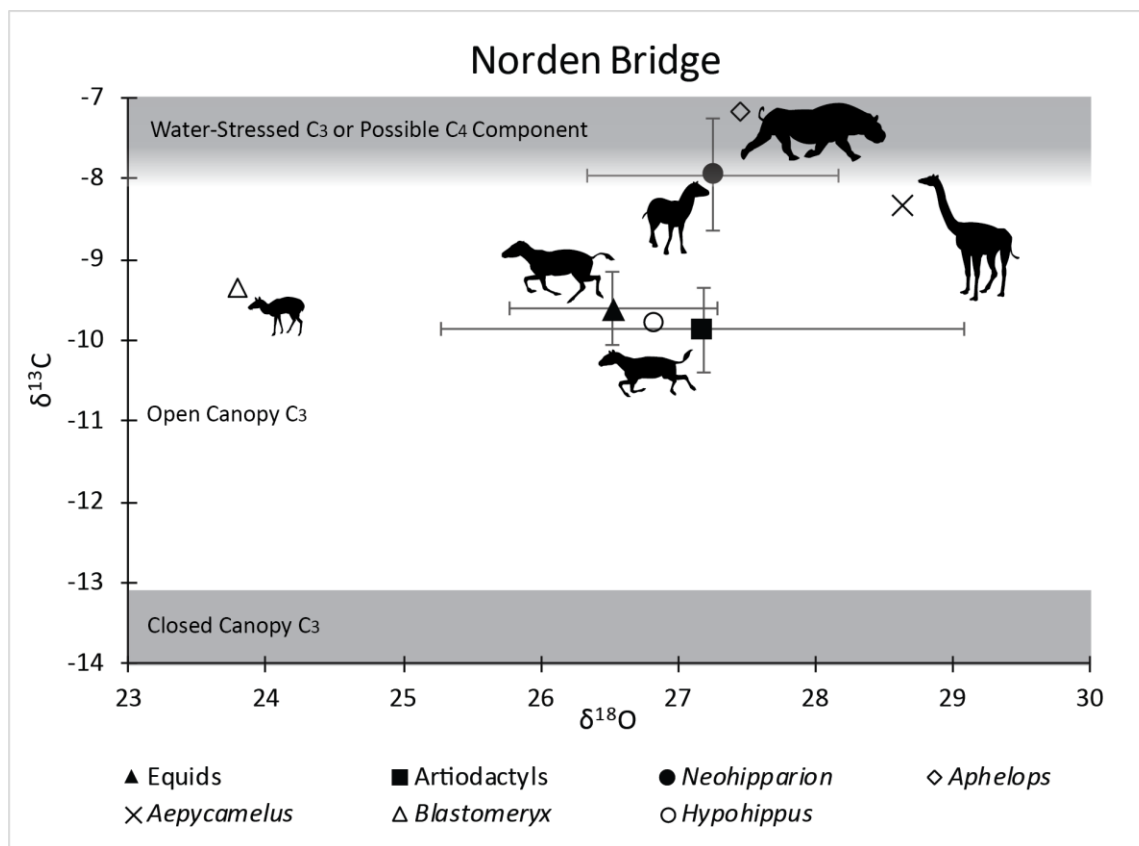


Figure 9. Mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for significant genera and reduced groups in Valentine Quarry with vegetation boundaries. Error on faunal averages represent 95% confidence of the mean of all individuals within that taxa ( $1.96 \times \text{S.E.}$ ).

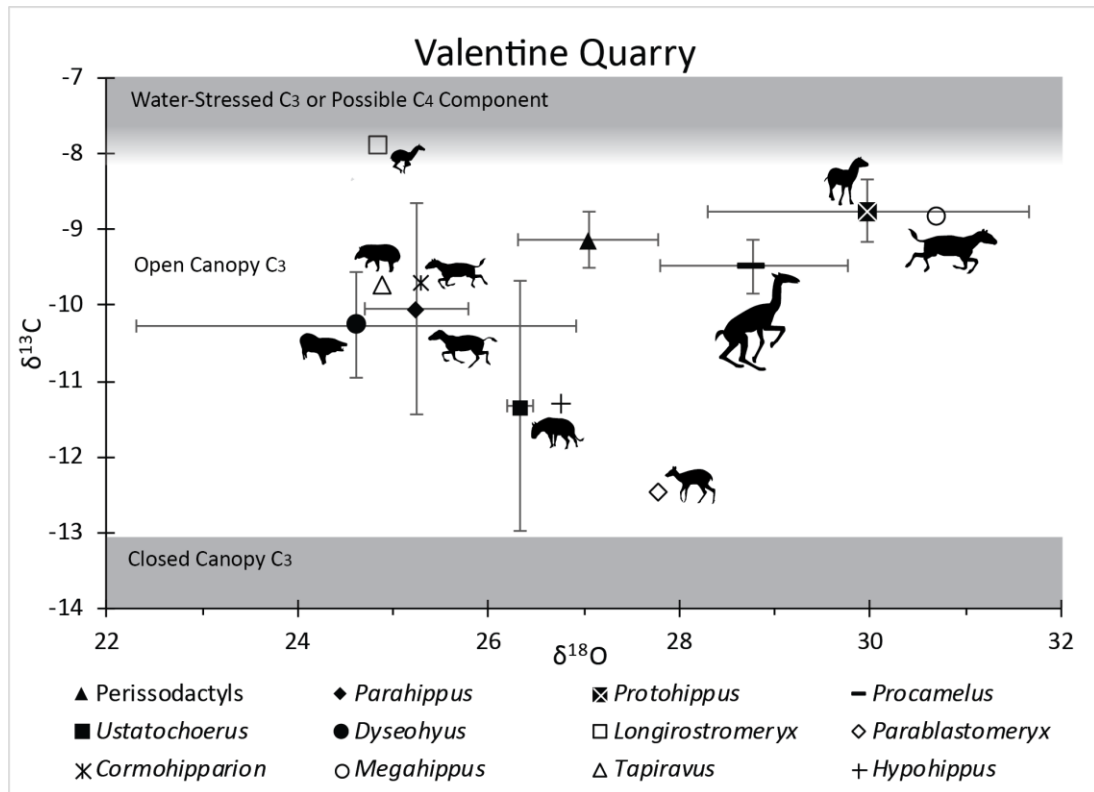


Figure 10. Mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of Nebraskan local faunas compiled from this study and from Kita *et al.* 2014 with vegetation boundaries. Error on local averages represent 95% confidence of the mean of all individuals within the local fauna ( $1.96 \times \text{S.E.}$ ).

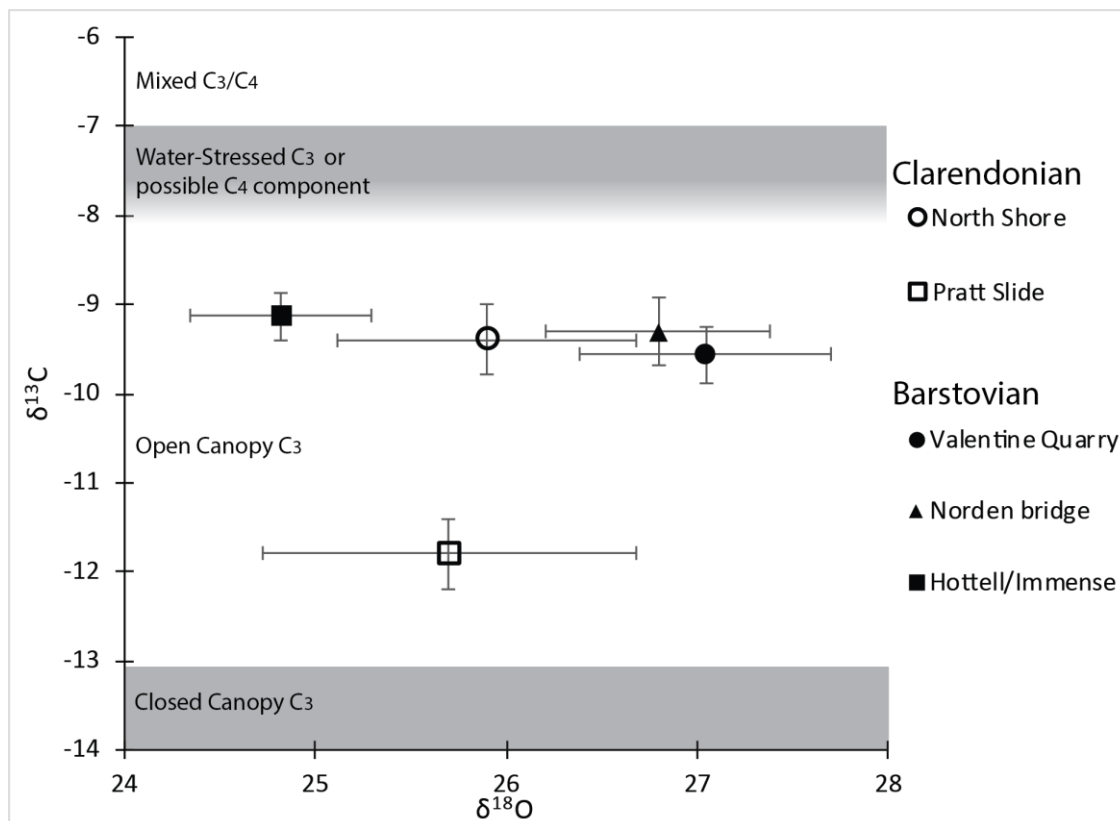


Table 1. Genera included in this study and the literature used to confirm identifications.

Fossils were also compared to representative specimens within the UNSM collections and holotypes when available.

| Order          | Family            | Genus   | Literature Used   |
|----------------|-------------------|---|---|
| Perissodactyla | Rhinocerotidae    | <i>Peraceras crassus</i><br><i>Teleoceras medicornutus</i><br><i>Aphelops megalodus</i>   | Prothero 1998, Mead 1999.   |
|                | Equidae           | <i>Megahippus mckennai</i><br><i>Hypohippus osborni</i><br><i>Parahippus cognatus</i><br><i>Merychippus insignis</i><br><i>Cormohipparion sp.</i><br><i>Neohipparion republicanus</i><br><i>Calippus placidus</i><br><i>Protohippus perditus</i><br><i>Pliohippus mirabilis</i> | Gidley 1907, Matthew 1926, Quinn 1955, Corner 1976, Hulbert and MacFadden 1990, Voorhies 1990b, MacFadden 1992, Woodburne 1996, MacFadden 1998. |
|                | Chalicotheridae   | undet.  | Coombs 1998.  |
|                | Tapridae          | <i>Tapiravus polkensis</i>  | Colbert and Schoch 1998   |
| Artiodactyla   | Merycoidodontidae | <i>Brachycrus sp.</i><br><i>Ticholeptus sp.</i><br><i>Ustatochoerus medius</i>  | Schultz and Falkenbach 1941, Macdonald 1956, Schultz and Falkenbach 1968, Stevens and Stevens 1998.   |

|  |                |  |  |
|--|----------------|--|--|
|  | Camelidae      | <i>Aepycamelus robustus</i><br><i>Procamelus occidentalis</i>                              | Corner 1976, Honey <i>et al.</i> 1998.                       |
|  | Tayassuidae    | <i>"Dyseohyus" xiphodonticus</i>   | Stock 1937, Corner 1976, Voorhies 1990b.                     |
|  | Dromomerycidae | <i>Rakomeryx sp.</i><br><i>Bouromeryx americanus</i>                                       | Frick 1937, Janis and Manning 1998, Prothero and Liter 2008. |
|  | Antilocapridae | <i>Merycodus minor</i>   | Frick 1937, Voorhies 1990b, Janis and Manning 1998.          |
|  | Leptomerycidae | <i>Pseudoparablastomeryx scotti</i>  | Webb 1998, Metais and Vislobokova 2007.                      |
|  | Moschidae      | <i>Parablastomeryx sp.</i><br><i>Blastomeryx gemnifer</i><br><i>Longiostromeryx blicki</i> | Corner 1976, Prothero 2007.                                  |



Table 2. Descriptive statistics for genera included in local faunas. Asterisks indicate combined groups used in the combined pairwise comparisons and include the taxa listed above the category.

| LF | Genus                         | n  | $\delta^{13}\text{C}(\text{VPDB})$ |            |               |           |                | $\delta^{18}\text{O}(\text{VSMOW})$ |            |               |          |              |
|----|-------------------------------|----|------------------------------------|------------|---------------|-----------|----------------|-------------------------------------|------------|---------------|----------|--------------|
|    |                               |    | Mean (‰)                           | Median (‰) | 1.96*S.E. (‰) | S. D. (‰) | Range (‰)      | Mean (‰)                            | Median (‰) | 1.96*S.E. (‰) | S.D. (‰) | Range (‰)    |
| HI | <i>Peraceras</i>              | 6  | -9.5                               | -9.6       | 0.6           | 0.6       | -10.4 to -8.8  | 23.5                                | 23.6       | 0.6           | 0.7      | 22.7 to 24.4 |
| HI | <i>Teleoceras</i>             | 6  | -9.9                               | -9.7       | 1.0           | 1.2       | -11.9 to -8.3  | 24.9                                | 24.5       | 1.6           | 1.8      | 23.2 to 28.1 |
| HI | <i>Hypohippus</i>             | 4  | -9.6                               | -9.7       | 0.7           | 0.6       | -10.1 to -8.7  | 24.5                                | 24.9       | 1.2           | 1.0      | 23.0 to 25.2 |
| HI | <i>Parahippus</i>             | 5  | -8.8                               | -8.8       | 0.2           | 0.2       | -9.1 to -8.5   | 25.9                                | 26.7       | 1.6           | 1.6      | 23.2 to 27.2 |
| HI | <i>Merychippus</i>            | 5  | -8.2                               | -8.3       | 0.9           | 0.9       | -9.2 to -7     | 25.1                                | 25.1       | 0.9           | 0.9      | 24.2 to 26.3 |
| HI | <i>Neohipparion</i>           | 5  | -8.5                               | -9.1       | 1.4           | 1.4       | -9.3 to -6.0   | 24.9                                | 24.7       | 1.0           | 1.1      | 23.6 to 26.0 |
| HI | <i>Tapiravus</i>              | 3  | -9.5                               | -9.2       | 1.0           | 0.7       | -10.3 to -9    | 25.0                                | 23.8       | 3.0           | 2.2      | 23.7 to 27.5 |
| HI | <i>Perissodactyls*</i>        | 34 | -9.1                               | -9.1       | 0.4           | 1.0       | -11.9 to -6.0  | 24.8                                | 24.6       | 0.5           | 1.4      | 22.7 to 28.1 |
| HI | <i>Cormohipparion</i>         | 1  | -8.2                               | -          | -             | -         | -              | 27.0                                | -          | -             | -        | -            |
| HI | <i>Chalicotheres</i>          | 1  | -9.1                               | -          | -             | -         | -              | 27.3                                | -          | -             | -        | -            |
| HI | <i>Brachycrus</i>             | 1  | -9.1                               | -          | -             | -         | -              | 28.5                                | -          | -             | -        | -            |
| HI | <i>Pseudoparablastomeryx</i>  | 3  | -9.5                               | -9.3       | 0.6           | 0.5       | -10.0 to -9.1  | 22.5                                | 21.9       | 2.0           | 1.5      | 21.5 to 24.2 |
| HI | <i>Merycodus</i>              | 6  | -9.2                               | -9.1       | 0.7           | 0.8       | -10.4 to -8.3  | 23.8                                | 23.8       | 0.8           | 0.9      | 22.5 to 24.9 |
| HI | <i>Rakomeryx</i>              | 3  | -9.2                               | -9.1       | 0.9           | 0.6       | -9.8 to -8.6   | 26.8                                | 26.1       | 2.1           | 1.5      | 25.8 to 28.6 |
|    | Hottel Ranch/ Immense Journey | 49 | -9.1                               | -9.1       | 0.3           | 0.9       | -11.9 to -6.0  | 24.8                                | 24.7       | 0.5           | 1.7      | 21.5 to 28.6 |
| NB | <i>Megahippus</i>             | 2  | -8.4                               | -8.4       | 0.4           | 0.2       | -8.5 to -8.3   | 27.8                                | 27.8       | 3.4           | 1.7      | 26.6 to 29.0 |
| NB | <i>Merychippus</i>            | 5  | -9.9                               | -9.5       | 0.9           | 1.1       | -11.3 to -8.6  | 25.7                                | 25.1       | 0.9           | 1.8      | 23.8 to 28.7 |
| NB | <i>Calippus</i>               | 5  | -9.9                               | -9.9       | 0.9           | 1.0       | -11.2 to -8.5  | 27.1                                | 27.1       | 0.8           | 0.8      | 25.7 to 27.9 |
| NB | <i>Protohippus</i>            | 5  | -9.5                               | -9.6       | 0.5           | 0.6       | -10.1 to -8.8  | 26.3                                | 25.9       | 1.6           | 1.7      | 24.3 to 28.8 |
| NB | <i>Equids*</i>                | 17 | -9.6                               | -9.6       | 0.5           | 0.9       | -11.3 to -8.2  | 26.5                                | 26.6       | 0.8           | 1.5      | 23.8 to 29.0 |
| NB | <i>Neohipparion</i>           | 5  | -8.0                               | -7.8       | 0.7           | 0.7       | -8.8 to -7.0   | 27.3                                | 27.2       | 0.9           | 0.9      | 25.8 to 28.2 |
| NB | <i>Hypohippus</i>             | 1  | -9.8                               | -          | -             | -         | -              | 26.8                                | -          | -             | -        | -            |
| NB | <i>Aphelops</i>               | 1  | -7.2                               | -          | -             | -         | -              | 27.5                                | -          | -             | -        | -            |
| NB | <i>Ticholeptus</i>            | 2  | -9.8                               | -9.8       | 2.5           | 1.3       | -10.7 to -8.9  | 28.5                                | 28.5       | 2.7           | 1.3      | 27.5 to 29.4 |
| NB | <i>Bouromeryx</i>             | 5  | -9.9                               | -10.2      | 0.5           | 0.5       | -10.3 to -9.2  | 26.7                                | 26.6       | 2.6           | 2.6      | 23.7 to 29.3 |
| NB | <i>Artiodactyls*</i>          | 7  | -9.9                               | -10.2      | 0.5           | 0.6       | -10.7 to -8.9  | 27.2                                | 27.5       | 1.9           | 2.4      | 23.7 to 29.4 |
| NB | <i>Aepycamelus</i>            | 1  | -8.3                               | -          | -             | -         | -              | 28.6                                | -          | -             | -        | -            |
| NB | <i>Blastomeryx</i>            | 1  | -9.4                               | -          | -             | -         | -              | 23.8                                | -          | -             | -        | -            |
|    | Norden Bridge Quarry          | 33 | -9.3                               | -9.4       | 0.4           | 1.1       | -11.3 to -7.0  | 26.8                                | 27.0       | 0.6           | 1.7      | 23.7 to 29.4 |
| VQ | <i>Peraceras</i>              | 3  | -9.6                               | -10.0      | 1.5           | 1.1       | -10.4 to -8.3  | 26.0                                | 25.9       | 1.5           | 1.1      | 24.9 to 27.1 |
| VQ | <i>Merychippus</i>            | 5  | -9.0                               | -8.8       | 0.9           | 0.9       | -10.4 to -7.9  | 27.8                                | 27.8       | 1.7           | 1.7      | 25.7 to 30.2 |
| VQ | <i>Calippus</i>               | 4  | -9.0                               | -9.0       | 0.6           | 0.5       | -9.5 to -8.5   | 26.8                                | 26.6       | 2.2           | 1.9      | 24.9 to 29.0 |
| VQ | <i>Pliohippus</i>             | 5  | -9.1                               | -9.5       | 0.7           | 0.7       | -9.8 to -8.2   | 27.1                                | 26.8       | 0.9           | 0.9      | 26.3 to 28.7 |
| VQ | <i>Perissodactyls*</i>        | 17 | -9.1                               | -9.1       | 0.4           | 0.8       | -10.4 to -7.9  | 27.1                                | 26.8       | 0.7           | 1.5      | 24.9 to 30.2 |
| VQ | <i>Parahippus</i>             | 4  | -10.1                              | -10.0      | 1.4           | 1.2       | -11.6 to -8.6  | 25.0                                | 25.1       | 0.5           | 0.5      | 24.5 to 25.5 |
| VQ | <i>Protohippus</i>            | 5  | -8.8                               | -8.9       | 0.4           | 0.4       | -9.2 to -8.3   | 30.0                                | 29.5       | 1.7           | 1.7      | 27.9 to 32.6 |
| VQ | <i>Megahippus</i>             | 1  | -8.8                               | -          | -             | -         | -              | 30.7                                | -          | -             | -        | -            |
| VQ | <i>Hypohippus</i>             | 1  | -11.3                              | -          | -             | -         | -              | 26.8                                | -          | -             | -        | -            |
| VQ | <i>Cormohipparion</i>         | 1  | -9.7                               | -          | -             | -         | -              | 25.3                                | -          | -             | -        | -            |
| VQ | <i>Tapiravus</i>              | 1  | -9.7                               | -          | -             | -         | -              | 24.9                                | -          | -             | -        | -            |
| VQ | <i>Procamelus</i>             | 5  | -9.5                               | -9.3       | 0.4           | 0.4       | -9.9 to -9.1   | 28.8                                | 29.0       | 1.0           | 1.0      | 27.1 to 29.8 |
| VQ | <i>Ustatochoerus</i>          | 2  | -11.3                              | -11.3      | 1.7           | 0.9       | -11.9 to -10.7 | 26.3                                | 26.3       | 0.1           | 0.1      | 26.3 to 26.4 |
| VQ | <i>Dyseohyus</i>              | 5  | -10.3                              | -10.1      | 0.7           | 0.7       | -11.1 to -10.0 | 24.6                                | 24.3       | 2.3           | 2.4      | 21.7 to 28.3 |
| VQ | <i>Parablastomeryx</i>        | 1  | -12.5                              | -          | -             | -         | -              | 27.8                                | -          | -             | -        | -            |
| VQ | <i>Longirostromeryx</i>       | 1  | -7.9                               | -          | -             | -         | -              | 24.9                                | -          | -             | -        | -            |
|    | Type Valentine Quarries       | 44 | -9.6                               | -9.4       | 0.3           | 1.1       | -12.5 to -7.9  | 27.0                                | 26.8       | 0.7           | 2.2      | 21.7 to 32.6 |

Table 3. Matrices of pairwise probabilities of mean differences in  $\delta^{13}\text{C}$  (left) and  $\delta^{18}\text{O}$  (right) between multiply sampled genera in each local fauna. Bold values indicate significant differences using Fisher's LSD post hoc ( $\alpha \leq 0.05$ ). An asterisk after a value indicates significant differences using Tukey's post hoc ( $\alpha \leq 0.05$ ).

| $\delta^{13}\text{C}, \delta^{18}\text{O}$ | 1                    | 2                            | 3                            | 4                     | 5                            | 6                     | 7                    | 8                   | 9                    | 10           |
|--|----------------------|------------------------------|------------------------------|-----------------------|------------------------------|-----------------------|----------------------|---------------------|----------------------|--------------|
| 1 Peraceras                                | 1.000, 1.000         |                              |                              |                       |                              |                       |                      |                     |                      |              |
| 2 Teleoceras                               | 0.588, 0.098         | 1.000, 1.000                 |                              |                       |                              |                       |                      |                     |                      |              |
| 3 Tapiravus                                | 0.916, 0.138         | 0.650, 0.934                 | 1.000, 1.000                 |                       |                              |                       |                      |                     |                      |              |
| 4 Hypohippus                               | 0.938, 0.098         | 0.686, 0.675                 | 0.875, 0.671                 | 1.000, 1.000          |                              |                       |                      |                     |                      |              |
| 5 Parahippus                               | 0.039, <b>0.009</b>  | 0.089, 0.378                 | 0.084, 0.551                 | 0.040, 0.182          | 1.000, 1.000                 |                       |                      |                     |                      |              |
| 6 Merychippus                              | 0.016, 0.007         | 0.029, 0.842                 | 0.075, 0.954                 | 0.034, 0.362          | 0.162, 0.371                 | 1.000, 1.000          |                      |                     |                      |              |
| 7 Neohipparion                             | 0.119, 0.023         | 0.106, 1.000                 | 0.284, 0.921                 | 0.184, 0.553          | 0.590, 0.299                 | 0.705, 0.775          | 1.000, 1.000         |                     |                      |              |
| 8 Merycodus                                | 0.382, 0.494         | 0.265, 0.216                 | 0.565, 0.268                 | 0.415, 0.327          | 0.407, <b>0.028</b>          | 0.094, 0.046          | 0.332, 0.102         | 1.000, 1.000        |                      |              |
| 9 Pseudoparablastomeryx                    | 0.867, 0.207         | 0.618, 0.090                 | 0.966, 0.180                 | 0.817, 0.094          | 0.033, <b>0.028*</b>         | 0.063, <b>0.020</b>   | 0.279, <b>0.036</b>  | 0.564, 0.150        | 1.000, 1.000         |              |
| 10 Rakomeryx                               | 0.450, <b>0.002*</b> | 0.403, 0.160                 | 0.600, 0.310                 | 0.452, 0.058          | 0.252, 0.450                 | 0.139, 0.082          | 0.433, 0.078         | 0.950, <b>0.007</b> | 0.553, <b>0.025*</b> | 1.000, 1.000 |
| NB   |                      |                              |                              |                       |                              |                       |                      |                     |                      |              |
| $\delta^{13}\text{C}, \delta^{18}\text{O}$ | 1                    | 2                            | 3                            | 4                     | 5                            | 6                     | 7                    |                     |                      |              |
| 1 Megahippus                               | 1.000, 1.000         |                              |                              |                       |                              |                       |                      |                     |                      |              |
| 2 Merychippus                              | 0.125, 0.235         | 1.000, 1.000                 |                              |                       |                              |                       |                      |                     |                      |              |
| 3 Neohipparion                             | 0.457, 0.606         | <b>0.010*</b> , 0.136        | 1.000, 1.000                 |                       |                              |                       |                      |                     |                      |              |
| 4 Calippus                                 | 0.094, 0.454         | 0.959, 0.180                 | <b>0.007*</b> , 0.725        | 1.000, 1.000          |                              |                       |                      |                     |                      |              |
| 5 Protohippus                              | 0.039, 0.332         | 0.512, 0.639                 | <b>0.004</b> , 0.282         | 0.508, 0.375          | 1.000, 1.000                 |                       |                      |                     |                      |              |
| 6 Ticholeptus                              | 0.262, 0.699         | 0.887, 0.120                 | <b>0.050</b> , 0.218         | 0.906, 0.137          | 0.720, 0.163                 | 1.000, 1.000          |                      |                     |                      |              |
| 7 Bouromeryx                               | <b>0.009</b> , 0.615 | 0.995, 0.533                 | <b>0.001*</b> , 0.650        | 0.949, 0.762          | 0.282, 0.785                 | 0.824, 0.416          | 1.000, 1.000         |                     |                      |              |
| VQ   |                      |                              |                              |                       |                              |                       |                      |                     |                      |              |
| $\delta^{13}\text{C}, \delta^{18}\text{O}$ | 1                    | 2                            | 3                            | 4                     | 5                            | 6                     | 7                    | 8                   | 9                    |              |
| 1 Peraceras                                | 1.000, 1.000         |                              |                              |                       |                              |                       |                      |                     |                      |              |
| 2 Parahippus                               | 0.591, 0.124         | 1.000, 1.000                 |                              |                       |                              |                       |                      |                     |                      |              |
| 3 Merychippus                              | 0.408, 0.150         | 0.122, <b>0.008</b>          | 1.000, 1.000                 |                       |                              |                       |                      |                     |                      |              |
| 4 Calippus                                 | 0.406, 0.542         | 0.130, 0.081                 | 0.882, 0.415                 | 1.000, 1.000          |                              |                       |                      |                     |                      |              |
| 5 Protohippus                              | 0.170, <b>0.012*</b> | <b>0.038</b> , <b>0.000*</b> | 0.678, 0.087                 | 0.413, <b>0.034</b>   | 1.000, 1.000                 |                       |                      |                     |                      |              |
| 6 Pliohippus                               | 0.506, 0.166         | 0.157, <b>0.002</b>          | 0.707, 0.433                 | 0.781, 0.744          | 0.309, <b>0.011</b>          | 1.000, 1.000          |                      |                     |                      |              |
| 7 Procamelus                               | 0.847, <b>0.010</b>  | 0.306, <b>0.000*</b>         | 0.258, 0.324                 | 0.163, 0.081          | 0.021, 0.216                 | 0.362, 0.026          | 1.000, 1.000         |                     |                      |              |
| 8 Ustatocboerus                            | 0.158, 0.694         | 0.190, 0.009                 | <b>0.024*</b> , 0.297        | <b>0.012*</b> , 0.764 | <b>0.002*</b> , <b>0.037</b> | <b>0.015*</b> , 0.311 | <b>0.007</b> , 0.022 | 1.000, 1.000        |                      |              |
| 9 Dyseohyus                                | 0.325, 0.395         | 0.699, 0.708                 | <b>0.035</b> , <b>0.039*</b> | <b>0.024</b> , 0.181  | <b>0.004</b> , <b>0.003*</b> | <b>0.036</b> , 0.059  | 0.062, <b>0.007*</b> | 0.147, 0.377        | 1.000, 1.000         |              |

Table 4. Matrices of pairwise probabilities of mean differences in  $\delta^{13}\text{C}$  (left) and  $\delta^{18}\text{O}$  (right) between multiply sampled genera in each local fauna. Genera with insignificant mean differences are combined into combined groups. Bold values indicate significant differences using Fisher's LSD post hoc ( $\alpha \leq 0.05$ ). An asterisk after a value indicates significant differences using Tukey's post hoc ( $\alpha \leq 0.05$ ).

| HI                  | 1                            | 2                            | 3                            | 4                    |              |              |
|---------------------|------------------------------|------------------------------|------------------------------|----------------------|--------------|--------------|
| 1 Perissodactyls    | 1.000, 1.000                 |                              |                              |                      |              |              |
| 2 Merycodus         | 0.958, 0.118                 | 1.000, 1.000                 |                              |                      |              |              |
| 3 Pseudoparablastom | 0.576, <b>0.013*</b>         | 0.564, 0.149                 | 1.000, 1.000                 |                      |              |              |
| 4 Rakomeryx         | 0.923, <b>0.023</b>          | 0.950, <b>0.007*</b>         | 0.553, <b>0.025*</b>         | 1.000, 1.000         |              |              |
| NB                  | 1                            | 2                            | 3                            |                      |              |              |
| 1 Equids            | 1.000, 1.000                 |                              |                              |                      |              |              |
| 2 Artiodactyls      | 0.509, 0.426                 | 1.000, 1.000                 |                              |                      |              |              |
| 3 Neohipparion      | <b>0.002*</b> , 0.329        | <b>0.001*</b> , 0.950        | 1.000, 1.000                 |                      |              |              |
| VQ                  | 1                            | 2                            | 3                            | 4                    | 5            | 6            |
| 1 Perissodactyls    | 1.000, 1.000                 |                              |                              |                      |              |              |
| 2 Parahippus        | <b>0.047</b> , <b>0.008</b>  | 1.000, 1.000                 |                              |                      |              |              |
| 3 Protohippus       | 0.299, <b>0.003*</b>         | <b>0.038</b> , <b>0.000*</b> | 1.000, 1.000                 |                      |              |              |
| 4 Procamelus        | 0.345, <b>0.025</b>          | 0.306, <b>0.000*</b>         | 0.021, 0.216                 | 1.000, 1.000         |              |              |
| 5 Ustatochcerus     | <b>0.001*</b> , 0.515        | 0.190, 0.009                 | <b>0.002*</b> , <b>0.037</b> | <b>0.007</b> , 0.515 | 1.000, 1.000 |              |
| 6 Dyseohyus         | <b>0.008</b> , <b>0.011*</b> | 0.699, 0.708                 | 0.004, <b>0.003*</b>         | 0.062, <b>0.011*</b> | 0.147, 0.377 | 1.000, 1.000 |

Table 5. Matrices of pairwise probabilities of mean difference in  $\delta^{13}\text{C}$  (left) and  $\delta^{18}\text{O}$  (right) between local faunas. Bold values indicate significant differences using Fisher's LSD post hoc ( $\alpha \leq 0.05$ ). An asterisk after a value indicates significant differences using Tukey's post hoc ( $\alpha \leq 0.05$ ).

| Local Faunas        | 1                    | 2            | 3            |
|---------------------|----------------------|--------------|--------------|
| 1. Hottell/ Immense | 1.000, 1.000         |              |              |
| 2. Norden Bridge    | 0.450, <b>0.000*</b> | 1.000, 1.000 |              |
| 3. Valentine Quarry | 0.042, <b>0.000*</b> | 0.302, 0.589 | 1.000, 1.000 |

Table 6. Matrices of pairwise probabilities of mean difference in  $\delta^{13}\text{C}$  (left) and  $\delta^{18}\text{O}$  (right) between Barstovian (HI, NB, VQ) and Clarendonian (NS, PS) local faunas from Kita *et al.* 2014. Bold values indicate significant differences using Fisher's LSD post hoc ( $\alpha \leq 0.05$ ). An asterisk after a value indicates significant differences using Tukey's post hoc ( $\alpha \leq 0.05$ ).

| Local Faunas        | 1                     | 2                            | 3                            | 4            | 5            |
|---------------------|-----------------------|------------------------------|------------------------------|--------------|--------------|
| 1. North Shore      | 1.000, 1.000          |                              |                              |              |              |
| 2. Pratt Slide      | <b>0.000*</b> , 0.800 | 1.000, 1.000                 |                              |              |              |
| 3. Hottell/ Immense | 0.237, <b>0.031</b>   | <b>0.000*</b> , 0.068        | 1.000, 1.000                 |              |              |
| 4. Norden Bridge    | 0.675, 0.069          | <b>0.000*</b> , <b>0.040</b> | 0.450, <b>0.000*</b>         | 1.000, 1.000 |              |
| 5. Valentine Quarry | 0.624, <b>0.046</b>   | <b>0.000*</b> , <b>0.023</b> | <b>0.042</b> , <b>0.000*</b> | 0.303, 0.589 | 1.000, 1.000 |

Table 7. Raw data from bulk sampling of enamel.

| Museum Number | Genus                  | Local Fauna     | $\delta^{13}\text{C}_{(\text{VPDB})}$ | $\delta^{18}\text{O}_{(\text{VPDB})}$ | $\delta^{18}\text{O}_{(\text{VSMOW})}$ |
|---------------|------------------------|-----------------|---------------------------------------|---------------------------------------|--|
| UNSM 135061   | <i>Brachycrus</i>      | Hottell/Immense | -9.1                                  | -2.3                                  | 28.5                                   |
| UNSM 133509   | <i>cf. Merychippus</i> | Hottell/Immense | -8.9                                  | -5.6                                  | 25.1                                   |
| UNSM 133510   | <i>cf. Merychippus</i> | Hottell/Immense | -8.3                                  | -4.4                                  | 26.3                                   |
| UNSM 133511   | <i>cf. Merychippus</i> | Hottell/Immense | -9.1                                  | -6.5                                  | 24.2                                   |
| UNSM 133512   | <i>cf. Merychippus</i> | Hottell/Immense | -7.0                                  | -6.3                                  | 24.4                                   |
| UNSM 133513   | <i>cf. Merychippus</i> | Hottell/Immense | -7.6                                  | -5.3                                  | 25.4                                   |
| UNSM 135057   | <i>Chalicotheres</i>   | Hottell/Immense | -9.1                                  | -3.5                                  | 27.3                                   |
| UNSM 117959   | <i>Cormohipparion</i>  | Hottell/Immense | -8.2                                  | -3.8                                  | 27.0                                   |
| UNSM 117957   | <i>Hypohippus</i>      | Hottell/Immense | -9.9                                  | -5.7                                  | 25.0                                   |
| UNSM 135051   | <i>Hypohippus</i>      | Hottell/Immense | -10.1                                 | -6.0                                  | 24.7                                   |
| UNSM 135052   | <i>Hypohippus</i>      | Hottell/Immense | -9.5                                  | -5.6                                  | 25.2                                   |
| UNSM 135953   | <i>Hypohippus</i>      | Hottell/Immense | -8.7                                  | -7.7                                  | 23.0                                   |
| UNSM 135070   | <i>Merycodus</i>       | Hottell/Immense | -9.8                                  | -6.7                                  | 24.0                                   |
| UNSM 135068   | <i>Merycodus</i>       | Hottell/Immense | -9.2                                  | -7.2                                  | 23.5                                   |
| UNSM 135067   | <i>Merycodus</i>       | Hottell/Immense | -8.3                                  | -5.9                                  | 24.9                                   |
| UNSM 135071   | <i>Merycodus</i>       | Hottell/Immense | -8.9                                  | -7.5                                  | 23.1                                   |
| UNSM 135069   | <i>Merycodus</i>       | Hottell/Immense | -10.4                                 | -8.1                                  | 22.5                                   |
| UNSM 135072   | <i>Merycodus</i>       | Hottell/Immense | -8.3                                  | -5.9                                  | 24.8                                   |
| UNSM 133504   | <i>Neohipparion</i>    | Hottell/Immense | -9.2                                  | -4.8                                  | 26.0                                   |
| UNSM 133505   | <i>Neohipparion</i>    | Hottell/Immense | -6.0                                  | -7.1                                  | 23.6                                   |
| UNSM 133506   | <i>Neohipparion</i>    | Hottell/Immense | -8.7                                  | -6.1                                  | 24.7                                   |
| UNSM 133507   | <i>Neohipparion</i>    | Hottell/Immense | -9.2                                  | -6.5                                  | 24.2                                   |
| UNSM 133508   | <i>Neohipparion</i>    | Hottell/Immense | -9.1                                  | -4.8                                  | 26.0                                   |
| UNSM 133500   | <i>Parahippus</i>      | Hottell/Immense | -8.9                                  | -7.5                                  | 23.2                                   |
| UNSM 133501   | <i>Parahippus</i>      | Hottell/Immense | -8.8                                  | -5.2                                  | 25.5                                   |
| UNSM 133502   | <i>Parahippus</i>      | Hottell/Immense | -8.8                                  | -4.1                                  | 26.7                                   |

|             |                              |                 |       |      |      |
|-------------|------------------------------|-----------------|-------|------|------|
| UNSM 133503 | <i>Parahippus</i>            | Hottell/Immense | -8.5  | -4.1 | 26.7 |
| UNSM 117958 | <i>Parahippus</i>            | Hottell/Immense | -9.1  | -3.6 | 27.2 |
| UNSM 121632 | <i>Peraceras</i>             | Hottell/Immense | -10.4 | -8.0 | 22.7 |
| UNSM 121634 | <i>Peraceras</i>             | Hottell/Immense | -8.8  | -6.9 | 23.8 |
| UNSM 121633 | <i>Peraceras</i>             | Hottell/Immense | -9.8  | -6.3 | 24.4 |
| UNSM 121631 | <i>Peraceras</i>             | Hottell/Immense | -9.9  | -7.9 | 22.8 |
| UNSM 121627 | <i>Peraceras</i>             | Hottell/Immense | -9.4  | -7.1 | 23.6 |
| UNSM 121930 | <i>Peraceras</i>             | Hottell/Immense | -8.9  | -7.0 | 23.7 |
| UNSM 135063 | <i>Pseudoparablastomeryx</i> | Hottell/Immense | -9.1  | -6.5 | 24.2 |
| UNSM 135062 | <i>Pseudoparablastomeryx</i> | Hottell/Immense | -9.3  | -8.7 | 21.9 |
| UNSM 135066 | <i>Pseudoparablastomeryx</i> | Hottell/Immense | -10.0 | -9.1 | 21.5 |
| UNSM 135056 | <i>Rakomeryx</i>             | Hottell/Immense | -9.1  | -2.3 | 28.6 |
| UNSM 135054 | <i>Rakomeryx</i>             | Hottell/Immense | -9.8  | -5.0 | 25.8 |
| UNSM 135055 | <i>Rakomeryx</i>             | Hottell/Immense | -8.6  | -4.7 | 26.1 |
| UNSM 135058 | <i>Tapiravus</i>             | Hottell/Immense | -10.3 | -3.3 | 27.5 |
| UNSM 135059 | <i>Tapiravus</i>             | Hottell/Immense | -9.2  | -6.9 | 23.8 |
| UNSM 135060 | <i>Tapiravus</i>             | Hottell/Immense | -9.0  | -7.0 | 23.7 |
| UNSM 122259 | <i>Teleoceras</i>            | Hottell/Immense | -9.5  | -6.5 | 24.3 |
| UNSM 122256 | <i>Teleoceras</i>            | Hottell/Immense | -8.3  | -7.1 | 23.6 |
| UNSM 122282 | <i>Teleoceras</i>            | Hottell/Immense | -10.1 | -2.7 | 28.1 |
| UNSM 122286 | <i>Teleoceras</i>            | Hottell/Immense | -9.5  | -5.2 | 25.6 |
| UNSM 122260 | <i>Teleoceras</i>            | Hottell/Immense | -11.9 | -6.0 | 24.7 |
| UNSM 122258 | <i>Teleoceras</i>            | Hottell/Immense | -9.8  | -7.5 | 23.2 |
|             |                              |                 |       |      |      |
| UNSM 54873  | <i>Aepycamelus</i>           | Norden Bridge   | -8.3  | -2.2 | 28.6 |
| UNSM 84631  | <i>Aphelops</i>              | Norden Bridge   | -7.2  | -3.4 | 27.5 |
| UNSM 83534  | <i>Blastomeryx</i>           | Norden Bridge   | -9.4  | -6.9 | 23.8 |
| UNSM 83506  | <i>Bouromeryx</i>            | Norden Bridge   | -9.2  | -6.3 | 24.4 |
| UNSM 83890  | <i>Bouromeryx</i>            | Norden Bridge   | -10.2 | -1.5 | 29.3 |

|            |                        |               |       |      |      |
|------------|------------------------|---------------|-------|------|------|
| UNSM 83505 | <i>Bouromeryx</i>      | Norden Bridge | -9.6  | -7.0 | 23.7 |
| UNSM 83507 | <i>Bouromeryx</i>      | Norden Bridge | -10.3 | -1.6 | 29.3 |
| UNSM 83514 | <i>Bouromeryx</i>      | Norden Bridge | -10.2 | -4.2 | 26.6 |
| UNSM 90596 | <i>Calippus</i>        | Norden Bridge | -10.1 | -5.0 | 25.7 |
| UNSM 53839 | <i>Calippus</i>        | Norden Bridge | -9.7  | -3.0 | 27.9 |
| UNSM 53845 | <i>Calippus</i>        | Norden Bridge | -9.9  | -3.2 | 27.7 |
| UNSM 84227 | <i>Calippus</i>        | Norden Bridge | -8.5  | -3.8 | 27.0 |
| UNSM 53846 | <i>Calippus</i>        | Norden Bridge | -11.2 | -3.7 | 27.0 |
| UNSM 84208 | <i>Hypohippus</i>      | Norden Bridge | -9.8  | -3.9 | 26.8 |
| UNSM 84206 | <i>Megahippus</i>      | Norden Bridge | -8.5  | -1.9 | 29.0 |
| UNSM 84205 | <i>Megahippus</i>      | Norden Bridge | -8.2  | -4.2 | 26.6 |
| UNSM 85041 | <i>Merychippus</i>     | Norden Bridge | -8.6  | -5.7 | 25.0 |
| UNSM 85053 | <i>Merychippus</i>     | Norden Bridge | -10.8 | -4.7 | 26.1 |
| UNSM 85082 | <i>Merychippus</i>     | Norden Bridge | -9.5  | -2.2 | 28.7 |
| UNSM 85189 | <i>Merychippus</i>     | Norden Bridge | -9.3  | -5.6 | 25.1 |
| UNSM 85060 | <i>Merychippus</i>     | Norden Bridge | -11.3 | -6.9 | 23.8 |
| UNSM 84069 | <i>Neohipparion</i>    | Norden Bridge | -7.6  | -2.8 | 28.0 |
| UNSM 84080 | <i>Neohipparion</i>    | Norden Bridge | -7.0  | -3.6 | 27.2 |
| UNSM 84082 | <i>Neohipparion</i>    | Norden Bridge | -8.8  | -4.9 | 25.8 |
| UNSM 84066 | <i>Neohipparion</i>    | Norden Bridge | -7.8  | -3.7 | 27.1 |
| UNSM 84172 | <i>Neohipparion</i>    | Norden Bridge | -8.5  | -2.7 | 28.2 |
| UNSM 90124 | <i>Protohippus</i>     | Norden Bridge | -9.3  | -4.9 | 25.8 |
| UNSM 90122 | <i>Protohippus</i>     | Norden Bridge | -9.6  | -6.4 | 24.3 |
| UNSM 90118 | <i>Protohippus</i>     | Norden Bridge | -10.0 | -2.0 | 28.8 |
| UNSM 90119 | <i>Protohippus</i>     | Norden Bridge | -8.7  | -4.9 | 25.9 |
| UNSM 84258 | <i>Protohippus</i>     | Norden Bridge | -10.1 | -4.2 | 26.6 |
| UNSM 85581 | cf. <i>Ticholeptus</i> | Norden Bridge | -10.7 | -3.3 | 27.5 |
| UNSM 85583 | cf. <i>Ticholeptus</i> | Norden Bridge | -8.9  | -1.4 | 29.4 |
|            |                        |               |       |      |      |

|             |                        |                  |       |      |      |
|-------------|------------------------|------------------|-------|------|------|
| UNSM 98396  | <i>Calippus</i>        | Valentine Quarry | -9.5  | -5.8 | 24.9 |
| UNSM 98395  | <i>Calippus</i>        | Valentine Quarry | -8.7  | -1.8 | 29.0 |
| UNSM 135073 | <i>Calippus</i>        | Valentine Quarry | -8.5  | -5.2 | 25.6 |
| UNSM 98391  | <i>Calippus</i>        | Valentine Quarry | -9.4  | -3.1 | 27.7 |
| UNSM 135088 | <i>cf. Dyseohyus</i>   | Valentine Quarry | -9.3  | -6.0 | 24.7 |
| UNSM 135090 | <i>cf. Dyseohyus</i>   | Valentine Quarry | -10.0 | -9.0 | 21.7 |
| UNSM 96908  | <i>cf. Dyseohyus</i>   | Valentine Quarry | -10.1 | -6.4 | 24.3 |
| UNSM 135089 | <i>cf. Dyseohyus</i>   | Valentine Quarry | -11.1 | -6.6 | 24.2 |
| UNSM 135087 | <i>cf. Dyseohyus</i>   | Valentine Quarry | -10.9 | -2.6 | 28.3 |
| UNSM 77020  | <i>Cormohipparion</i>  | Valentine Quarry | -9.7  | -5.5 | 25.3 |
| UNSM 135094 | <i>Hypohippus</i>      | Valentine Quarry | -11.3 | -4.0 | 26.8 |
| UNSM 135095 | <i>Longiostromeryx</i> | Valentine Quarry | -7.9  | -5.9 | 24.9 |
| UNSM 135091 | <i>Megahippus</i>      | Valentine Quarry | -8.8  | -0.2 | 30.7 |
| UNSM 100374 | <i>Merychippus</i>     | Valentine Quarry | -8.5  | -4.0 | 26.7 |
| UNSM 100383 | <i>Merychippus</i>     | Valentine Quarry | -9.1  | -0.7 | 30.2 |
| UNSM 100376 | <i>Merychippus</i>     | Valentine Quarry | -8.8  | -2.1 | 28.8 |
| UNSM 100379 | <i>Merychippus</i>     | Valentine Quarry | -10.4 | -5.0 | 25.7 |
| UNSM 100378 | <i>Merychippus</i>     | Valentine Quarry | -7.9  | -3.0 | 27.8 |
| UNSM 135098 | <i>Parablastomeryx</i> | Valentine Quarry | -12.5 | -3.0 | 27.8 |
| UNSM 135078 | <i>Parahippus</i>      | Valentine Quarry | -8.6  | -5.4 | 25.3 |
| UNSM 135076 | <i>Parahippus</i>      | Valentine Quarry | -10.1 | -6.2 | 24.5 |
| UNSM 135075 | <i>Parahippus</i>      | Valentine Quarry | -10.0 | -5.9 | 24.8 |
| UNSM 135077 | <i>Parahippus</i>      | Valentine Quarry | -11.6 | -5.2 | 25.5 |
| UNSM 98339  | <i>Peraceras</i>       | Valentine Quarry | -8.3  | -4.8 | 25.9 |
| UNSM 135079 | <i>Peraceras</i>       | Valentine Quarry | -10.4 | -3.7 | 27.1 |
| UNSM 135080 | <i>Peraceras</i>       | Valentine Quarry | -10.0 | -5.8 | 24.9 |
| UNSM 100328 | <i>Pliohippus</i>      | Valentine Quarry | -8.2  | -3.7 | 27.1 |
| UNSM 100311 | <i>Pliohippus</i>      | Valentine Quarry | -9.5  | -4.5 | 26.3 |
| UNSM 100317 | <i>Pliohippus</i>      | Valentine Quarry | -9.6  | -4.2 | 26.6 |



|             |                      |                  |       |      |      |
|-------------|----------------------|------------------|-------|------|------|
| UNSM 100316 | <i>Pliohippus</i>    | Valentine Quarry | -8.7  | -2.2 | 28.7 |
| UNSM 98416  | <i>Pliohippus</i>    | Valentine Quarry | -9.8  | -3.9 | 26.8 |
| UNSM 98272  | <i>Procamelus</i>    | Valentine Quarry | -9.9  | -1.8 | 29.1 |
| UNSM 94136  | <i>Procamelus</i>    | Valentine Quarry | -9.8  | -1.1 | 29.8 |
| UNSM 94143  | <i>Procamelus</i>    | Valentine Quarry | -9.1  | -1.9 | 28.9 |
| UNSM 94144  | <i>Procamelus</i>    | Valentine Quarry | -9.2  | -3.7 | 27.1 |
| UNSM 135086 | <i>Procamelus</i>    | Valentine Quarry | -9.3  | -1.9 | 29.0 |
| UNSM 135084 | <i>Protohippus</i>   | Valentine Quarry | -9.1  | -1.4 | 29.5 |
| UNSM 135081 | <i>Protohippus</i>   | Valentine Quarry | -8.3  | -0.4 | 30.5 |
| UNSM 135082 | <i>Protohippus</i>   | Valentine Quarry | -8.4  | -1.4 | 29.5 |
| UNSM 135083 | <i>Protohippus</i>   | Valentine Quarry | -8.9  | -2.9 | 27.9 |
| UNSM 135085 | <i>Protohippus</i>   | Valentine Quarry | -9.2  | 1.6  | 32.6 |
| UNSM 98383  | <i>Tapiravus</i>     | Valentine Quarry | -9.7  | -5.8 | 24.9 |
| UNSM 135092 | <i>Ustatochoerus</i> | Valentine Quarry | -11.9 | -4.5 | 26.3 |
| UNSM 135093 | <i>Ustatochoerus</i> | Valentine Quarry | -10.7 | -4.4 | 26.4 |