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NEW STABLE ISOTOPE RECORD OF PALEOECOLOGICAL CHANGE IN THE
LATE NEOGENE OF THE WESTERN GREAT PLAINS FROM ENAMEL IN
LARGE MAMMALS

by

Zachary A. Kita

A THESIS

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Zachary A. Kita, M.S.

University of Nebraska, 2011

Adviser: Ross Secord

An expansion of C_4 grasslands occurred between 6 and 8 million years ago in the Great Plains of North America, as evidenced by a marked shift to more ^{13}C -enriched carbon isotope compositions from large fossil mammal tooth enamel and paleosol carbonates. Prior to this expansion, habitats were comprised of exclusively C_3 vegetation. To explore this problem I present a compilation of bulk stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope values from a variety of large mammals from 6 localities that span from the late Clarendonian to the late Blancan in Nebraska. As expected, late Miocene taxa had $\delta^{13}\text{C}$ values indicating that they exclusively exploited C_3 vegetation with habitats ranging from open forests in northern Nebraska to C_3 grasslands in southwest Nebraska. A shift to higher $\delta^{13}\text{C}$ values occurs in Pliocene camelids, equids, and gomphotheres suggesting that they began to consume C_4 vegetation. In contrast, a peccary (*Platygonus* sp.) still consumed only C_3 vegetation indicating that C_3 niches were still present. Through this Miocene-Pliocene transition there is an overall shift to lower $\delta^{18}\text{O}$ values in tooth enamel suggesting a long-term decrease in mean annual temperature. This agrees with previous work in the Great Plains and the marine realm. In addition, $\delta^{18}\text{O}$ values from serial samples suggest that seasonality decreased from the Miocene to

the Pliocene. These data agree with previous studies indicating global change in climate and vegetation from the late Miocene to the Pliocene.

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INTRODUCTION

The Earth underwent significant climate and environmental changes during the Neogene. Key events during this time include: intensified Antarctic glaciation starting at 15 Ma (Lear et al., 2000); progressive closure of the Panamanian straits from about 13 to about 2 Ma (Haug and Tiedemann, 1998); global expansion of C₄ biomass between 6 and 8 Ma (Cerling et al., 1993; Wang et al., 1994; MacFadden and Cerling, 1996; Cerling et al., 1997; Latorre et al., 1997; Passey et al., 2002; Fox and Koch, 2004); Mediterranean Sea desiccation as a result of the Messinian salinity crisis starting approximately 6 Ma and subsequent refilling through the Zanclean flooding 5.33 Ma (Hsü et al., 1973; Garcia-Castellanos et al., 2009); permanently increased Antarctic glaciation about 5 Ma (Lear et al., 2000); increased rates of uplift in the Himalayan and Andean Mountains as well as the Tibetan Plateau beginning about 5 Ma (Raymo et al., 1988); and the onset of Northern Hemisphere glaciation in the late Pliocene (Raymo, 1994).

The late Miocene to Pliocene also saw a period of worldwide faunal change. Significant turnover can be seen in faunas from Pakistan, North America, South America, Europe, and Africa (Cerling et al., 1997). Many woodland-adapted mammals were replaced by more open-habitat representatives and many brachydont taxa were replaced with taxa that were more hypsodont (Barry, 1995; Leakey et al., 1996). A time of relative stability represented by the Clarendonian chronofauna (late Miocene) in North America preceded a decrease in mammalian diversity through the disappearance of approximately two-thirds of mammalian genera from 15 to 2 Ma (Janis et al., 2000; Janis et al., 2002; Janis et al., 2004). In addition, mammalian clades including the oreodonts,

chalicotheres, and rhinoceroses disappeared from the Great Plains during this time (Janis et al., 1998).

The Reconstruction of terrestrial paleoenvironments and the diets of ancient mammalian herbivores in the North American Great Plains of the late Neogene is a critical step towards the improved understanding of faunal turnover and adaptation in this region. Resource partitioning has been studied in both modern and ancient environments where a mixture of C_3 and C_4 plants is present (DeNiro and Epstein, 1978; Vogel, 1978; Wang et al., 1994; MacFadden and Cerling, 1996; Koch, 1998; Feranec and MacFadden, 2006). Diet and habitat use are aspects of resource partitioning which may be revealed through stable isotope analysis (Koch et al., 1989; Fricke and O'Neil, 1996; Balasse et al., 2003; Feranec and MacFadden, 2006). However, resource partitioning has rarely been shown in C_3 -dominated communities isotopically (Feranec and MacFadden, 2006; Feranec, 2007; Secord et al., 2008). I aim to look at both C_3 -dominated communities and communities that include C_4 vegetation.

The goal of this research project is to establish a geochemical record from the Great Plains through the expansion of C_4 biomass and general cooling of the Pliocene that will reflect global, regional, and local histories of climate and ecological change. I address the following questions: (1) can stable isotope values from large samples of ancient mammal teeth reveal resource partitioning in C_3 -dominated paleoenvironments in the Great Plains? (2) were there enough patches of C_3 habitat remaining after the expansion of C_4 grasses to support C_3 browsers? (3) did camelids, proboscideans, and tayassuids respond to the expansion of C_4 grasslands by switching to a partial or dominant C_4 diet in a similar fashion to equids?

BACKGROUND

Geologic Context

The geographic distribution of sample localities and their stratigraphic relationships are shown in Figure 1. The relative ages of fossils analyzed in this study were estimated by their placement in North American land-mammal ages using data from Repenning (1987) and Voorhies (1990). Land-mammal ages constitute a biochronologic system based on the age and succession of mammalian evolutionary events in North America (Lindsay, 2003). Boundaries and subdivisions for each of these biochronologic are defined on the basis of mammalian evolutionary events loosely tied to stratal succession (Wood et al., 1941; Woodburne, 2004). In practice, many mammal ages are defined on the basis of immigrant taxa and are effectively interval chrons with boundaries established at first appearance datums.

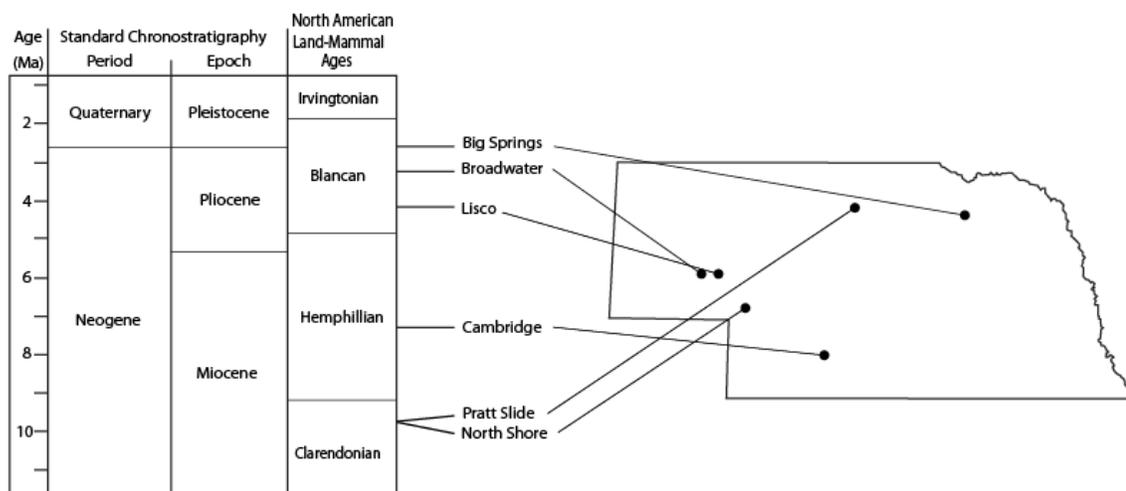


Figure 1: Generalized diagram showing the geochronologic sequence of Nebraska fossil localities, timing of North American land-mammal ages, and geographic distribution of fossil localities sampled in this study. Compiled using data from Repenning (1987), Voorhies (1990), and Passey et al. (2002).

This study focuses on six localities; three from the Ogallala Group of late Miocene age and three from the Broadwater Formation of Pliocene age. The Ogallala Group consists of the Pratt Slide and North Shore localities of late Clarendonian age and the Cambridge locality of medial Hemphillian age (Voorhies, 1990; Passey et al., 2002). The Broadwater Formation consists of the Lisco locality of early Blancan age, Broadwater locality of medial Blancan age, and Big Springs locality of late Blancan age (Repenning, 1987; Passey et al., 2002). All deposits sampled in this study are of fluvial or fluvio-lacustrine origin, and all but Lisco yield fish bones indicating that they accumulated in or near oxygenated water (Passey et al., 2002). The Pratt Slide locality is within the fill of a channel cut through the older Merritt Dam and Cap Rock members of the Ash Hollow Formation and the Burge and Devil's Gulch Members of the Valentine Formation (Skinner and Johnson, 1984). The Cambridge locality is the fill of a channel deeply incised into Cretaceous rock (Voorhies, 1990). Fossiliferous deposits at the Lisco locality are lenses of fine sand within the Broadwater Formation, which were deposited in abandoned channels or on floodplains (Swinehart, 1979). The Broadwater locality is a high terrace fill with a very thick gravel unit (Schultz and Stout, 1945; Howe, 1970), and the Big Springs locality is a gravel containing granite and anorthosite clasts from the Laramie Mountains (Stanley and Wayne, 1972).

Systematic Paleontology

Institution Abbreviations

AMNH	The American Museum of Natural History
F: AM	Frick Collection – American Museum of Natural History
TMM	Texas Memorial Museum
UCMP	University of California Museum of Paleontology
UNSM	University of Nebraska State Museum
UTBEG	University of Texas Bureau of Economic Geology
YPM – PU	Yale Peabody Museum – Princeton University

Order PERISSODACTYLA Owen, 1848

Family EQUIDAE Gray, 1872

CORMOHIPPARION Skinner and MacFadden, 1977

Cormohipparion occidentale (Skinner and MacFadden, 1977)

Holotype – ANSP 11287, four left and one right upper cheek teeth from the Xmas Quarry of the Ash Hollow Formation in Cherry County, Nebraska.

Description – Holotype described thoroughly in Skinner and MacFadden (1977) and Woodburne (2007).

Discussion – The UNSM specimens were included in a faunal list as *Neohipparion occidentale* by Voorhies (1990), but were not formally described until

Leite (1990) described them as *Cormohipparion occidentale*. *Cormohipparion occidentale*, as described by Skinner and MacFadden (1977), is characterized by an oval to slightly flattened protocone that remains isolated nearly to the base of the crown, a deep hypoconal groove persisting to the base of the crown, moderately to very complexly plicated fossette margins, and simple to moderately folded pli caballin. The Shape of the protocone in the North Shore sample varies from flattened with angular anterior and posterior ends to elliptical. Lower premolars and molars have metaconid and metastylid of nearly equal size. Most lower premolars have metaconid and metastylid separated from the protolophid by a narrow isthmus. *Cormohipparion occidentale* is larger in size and has higher crowned teeth than both *Cormohipparion goorisi* and *Cormohipparion sphenodus*. North Shore specimens look identical to *C. occidentale* from Hans Johnson Quarry and Xmas Quarry from the late Clarendonian of Nebraska (MacFadden, 1984).

Referred Specimens – **North Shore** (Kh-106): UNSM 94365, R M₂; 94382, L P⁴; 94394, L M₃; 97040, R M₂; 97044, M₃ fragment.

Cormohipparion sp.

Description – Similar to specimens described in Skinner and MacFadden (1977) and similar to UNSM specimens of *Cormohipparion occidentale* described by Leite (1990).

Discussion – UNSM specimens were identified by Michael Voorhies. Teeth are hypsodont with shallow ectoflexids and moderately developed pli caballinids in the lower premolars. Specimens look similar to *Cormohipparion occidentale* from North Shore

locality and from the Hans Johnson Quarry and Xmas Quarry from the late Clarendonian of north-central Nebraska (MacFadden, 1984), except that enamel plications do not seem as complex and the size of the teeth do not seem to be quite as large as the North Shore samples. These could just be within the range of variability for the species, but the limited number of specimens makes distinction of species very difficult. The presence of only teeth prevents use of other characteristics to distinguish species, so further collecting from this locality could help in species determination.

Referred Specimens – **Pratt Slide** (Bw-123): 117939, L P³; 117940, R P⁴.

HIPPARION Cristol, 1832

Hipparion sp.

Description – Generic description in MacFadden (1980) and MacFadden (1984).

Discussion - UNSM specimens identified by Michael Voorhies. Described as a medium-sized, mesocephalic, and moderately hypsodont horse. In the upper cheek teeth, the protocone is oval shaped. In contrast to the *Neohipparion* species seen in Cambridge, *Hipparion* exhibits smaller protocones, deeper ectoflexids, and well-developed pli caballinids. In contrast to the *Cormohipparion occidentale* from North Shore and most species of *Neohipparion*, *Hipparion* has less elongated protocones. Pratt Slide specimens of *Hipparion* are very similar in size based on dentition to *Hipparion tehonense* from the Trail Side Kat Quarry Channel of the late Clarendonian of north-central Nebraska (MacFadden, 1984). Unfortunately, the lack of a skull to compare the nasal notch or the dorsal preorbital fossa makes narrowing to a species very difficult.

Referred specimens – **Pratt Slide** (Bw-123): UNSM 5018-89A, L M₃; 5024-89B, R M₃; 5024-89C, R M₃.

NEOHIPPARION Gidley, 1903

Neohipparion eurystyle (Cope, 1893)

Holotype – TMM 40289-1, molar or premolar from Palo Duro Canyon in the Texas Panhandle.

Description – Holotype described thoroughly in MacFadden (1984).

Discussion – UNSM collections were identified by Bruce MacFadden and included in the faunal list by Voorhies (1990). The common horse in the Cambridge locality sample is this hipparionine that is slightly larger and more hypsodont than *Cormohipparion occidentale* in the North Shore locality. It shares the generic characters of separate elliptical protocone, moderately complex fossette plications, and widely spaced metaconid and metastylid. The species *N. eurystyle* is distinguished by its greater size, by an elliptical, but somewhat less elongate protocone with less pointed ends, prominent hypoconal groove, and presence of a pli caballinid. The pli caballinid is often double and the fossettes are complexly plicated.

These specimens match those described and figured as *Neohipparion eurystyle* by MacFadden (1984) from the late Hemphillian Ogallala Formation near Channing, Texas. *Neohipparion eurystyle* metapodials are long and slender and have proximo-lateral scars from articulation with the lateral metapodials. *N. eurystyle* is tridactyl, in contrast with the larger monodactyl *Pliohippus* that is seen rarely in this locality.

Referred specimens – **Cambridge** (Ft-40): UNSM 2988, L M₃; 4015, L M³; 4016, R M³; 4017, L M³; 4071, R M₃.

CALIPPUS Matthew and Stirton, 1930

Calippus sp.

Description – UNSM collections described in Leite (1990) and Breyer (1981).

Discussion – UNSM specimens identified by King Arthur Richey and included in the faunal list by Voorhies (1990). *Calippus* sp. is differentiated by the other major equid in the Cambridge locality by its size. *Calippus* is a pliohippine characterized by its small size. In addition, the genus is identified by upper premolars and molars with connected protocones and very simple fossette borders. The incisors are distinctively spatulate in shape. The Cambridge specimens of *Calippus* are larger than both *Calippus placidus* and *Calippus regulus* (Webb, 1969) and compare in size with Oshkosh and Box T local faunas as described in Breyer (1981).

Referred specimens – **Cambridge** (Ft-40): UNSM 4162, L M²; 4179, R M^x.

EQUUS Linnaeus, 1758

Equus simplicidens (Cope, 1892)

Holotype - TMM 40282-6, left M¹, from Mount Blanco in Crosby County, Texas.

Description – Holotype described in Cope (1892) and described further in Azzaroli and Voorhies (1993).

Discussion – UNSM specimens were included in the faunal list as *Plesippus* by Schultz and Stout (1945), as *Equus* by Voorhies (1987a), and identified and described thoroughly in Howe (1970). *Equus simplicidens* is larger than any other equid in this study. The fossettes are moderately wide and the enamel borders are relatively simple. Pli caballin and pli protocone are present. The M^3 is elongate and the mesostyle of the P^2 is very heavy with the parastyle compressed. There is a fairly large range in sizes of *Equus simplicidens* from the Broadwater locality (Howe, 1970) and the *E. simplicidens* specimens from the Big Springs locality all sit near the larger range of spectrum.

Referred specimens – **Broadwater** (Mo-5): UNSM 122056, R M^2 ; 2528-41, R M^3 . **Big Springs** (Ap-103): UNSM 46810, L M^3 ; 46848, L M_3 ; 46849, R M_3 ; 52140, L M^3 ; 4143-86, R M_3 ; 2043-92, L M^3 .

Family RHINOCEROTIDAE

TELEOCERAS Hatcher, 1894

Teleoceras major (Hatcher, 1894)

Holotype – YPM - PU 10645, a partial skull and right ramus, from Turtle Canyon in Sheridan County, Nebraska.

Description – Holotype described thoroughly in Prothero (2005).

Discussion – UNSM specimens were included in the faunal list by Voorhies (1990) and identified and described in Leite (1990). The most complete rhinoceros dentition in the North Shore locality is a partial palate. It agrees in morphology and size with several individuals in the large sample from the late Clarendonian Poison Ivy

Quarry referred to *T. major* by Voorhies and Thomasson (1979). In comparison to the less abundant rhinocerotids, *Aphelops*, cheek teeth of *Teleoceras* are more hypsodont and premolars are reduced in size relative to the molars while the premolars of *Aphelops* are large and molariform. *Teleoceras* has a partly restricted protocone on the upper molars. *Teleoceras* has upper incisors while *Aphelops* lacks them. The limb bones, particularly the metapodials, of *Teleoceras* are short and heavy in comparison with the less specialized limb elements of *Aphelops*. *Teleoceras major* is much smaller in size than *Teleoceras fossiger* from the Cambridge locality.

Referred specimens – **North Shore** (Kh-106): UNSM 94295, L M₂; 97071, R dentary fragment with R P₄; 97072, R P₄; 8176-92, L M₃; 8962-92, R P₄. **Pratt Slide** (Bw-123): 2112-94, L M³; 5018-89, R P⁴.

Teleoceras fossiger (Cope, 1878)

Holotype – AMNH 8390, a skull missing the left maxilla and much of the anterodorsal skull roof, from the early Hemphillian Beaver Creek area, Decatur County, Kansas.

Description – Holotype fully described in Osborn (1898), Osborn and Wortman (1898), and by Cope (1915).

Discussion – UNSM specimens were identified by Voorhies and included in the faunal list by Voorhies (1990) as *Teleoceras shultzi* (= *T. fossiger*). *Teleoceras fossiger* is more robust than the *Teleoceras major* specimens from the North Shore and Pratt Slide

localities. *Teleoceras fossiger* is the largest species of the genus and is well known from the Midwest.

Referred specimens – **Cambridge** (Ft-40): UNSM 5819, L M²; 5820A, L M³; 5820B, L M³; 5821, R M³.

APHELOPS Owen, 1845

Aphelops mutilus (Matthew, 1924)

Holotype – AMNH 17584, complete uncrushed skull, middle Hemphillian *Aphelops* Draw locality, Nebraska.

Description – Holotype thoroughly described in Matthew and Stirton (1932) and expanded on in Prothero (2005).

Discussion – UNSM specimens were identified by Michael Voorhies and included in the faunal list by Voorhies (1990) as *Aphelops kimballensis* (= *A. mutilus*). These rhinocerotids were once thought to be *Aphelops kimballensis* from the Kimballian land-mammal age (Tanner, 1967). This age has since been determined to be part of the Hemphillian and this rhinocerotid has been reclassified as *Aphelops mutilus*. The description of this taxon matches that of *A. mutilus* very well with regards to size, elevation of occiput, hypsodonty, retraction of narial notch, and the development of cristae (Prothero, 2005). In fact, the M¹⁻³ length for *A. kimballensis* in the Cambridge locality (167 mm) is identical with the same dimension in the type of *A. mutilus*. *A. mutilus* is the largest species in the genus. The teeth of *A. mutilus* are more hypsodont than other species including the generic *Aphelops* from the North Shore locality of the

late Clarendonian. In addition, the teeth have a more complicated pattern than other species in the genus.

Referred Specimens – **Cambridge** (Ft-40): UNSM 5812, R P₃; 1187-47, R P₃.

Aphelops sp.

Description – Generic characteristic described in Prothero (2005).

Discussion – UNSM specimens were included in the faunal list by Voorhies (1990) and identified and described in Leite (1990). By far the less common of the two North Shore rhinoceroses. It is represented mostly by isolated cheek teeth and incomplete limb bones. The scant material indicates a smaller species than *A.cf. mutilus* represented in the Cambridge locality as described in Leite (1990).

Referred Specimens – **North Shore** (Kh-106): UNSM 97050, R P³; 97051, R P⁴; 8286-92, R P³.

Order PROBOSCIDEA Illiger, 1811

Family GOMPHOTHERIIDAE Hay, 1922

SERBELODON Frick, 1933

Serbelodon cf. *S. barbourensis* (Frick, 1933)

Holotype- F:AM 25728, mandible and partial cranium, from Xmas Quarry in Cherry County, Nebraska in the Ash Hollow formation.

Description – Very similar to the description of Holotype by Frick (1933).

Discussion – UNSM specimens included in the faunal list by Voorhies (1990) and originally identified and described as *Amebelodon barbourensis* in Leite (1990) based on the description by Tobien (1972). This name has fallen out of favor and the original genus, *Serbelodon*, is now used. Assignment of this gomphothere to the genus *Serbelodon* is based upon its semi-flattened lower tusks, the presence of 5 ½ lophes on the M₃ and 4 ½ lophes on the M³, and 3 lophes on both upper and lower M². *S. barbourensis*, with its smaller, less flattened lower incisors appears to be less derived than the Hemphillian species *Amebelodon fricki* which may be the terminal form of the shovel-tusk lineage (Webb et al. 1981).

Referred Specimens – **North Shore** (Kh-106): UNSM 1001-02, tooth fragment; 1193-000, tooth fragment.

STEGOMASTODON Pohlig, 1912

Stegomastodon sp.

Description – Described in Osborn (1936) and Tobien (1973).

Discussion - UNSM specimens identified by Michael Voorhies and included in the faunal list by Schultz and Stout (1945) and Voorhies (1987a). Cheek teeth in *Stegomastodon* are characterized by secondary trefoiling, ptychodonty, the presence of many tubercles within the lophes, and an abundance of cement (much more than *Serbelodon* or other gomphotheres. Big Springs specimens are probably more closely related to the Pliocene species, *Stegomastodon mirificus*, than the earlier species from the

Miocene to early Pliocene, *Stegomastodon primitives* (Tobien, 1973), but limited specimens makes species determination difficult.

Referred specimens – **Big Springs** (Ap-103): UNSM 27556, molar fragment; 3061-98, L M₃.

Order ARTIODACYLA Owen, 1848

Family CAMELIDAE Gray, 1821

MEGATYLOPUS Matthew and Cook, 1909

Megatylopus cf. *M. primaevus* (Patton, 1969)

Holotype- UTBEG 31081-460, a left mandible, with P₂ alveolus, P₃-M₃. Farish Ranch, Bee County, Texas.

Description – Holotype described by Patton (1969).

Discussion – UNSM specimens were included in the faunal list by Voorhies (1990) and described and identified in Leite (1990). This is a very large camel with large, relatively hypsodont teeth and reduction in number and size of premolars.

Megatylopus is the oldest of the giant Camelini (Harrison, 1985) and *M. primaevus* is the most primitive species in the genus (Patton, 1969). It is the most common camel in the North Shore locality. It is distinguished from the only other Clarendonian giant camel, *Aepycamelus*, by having shorter limbs, more hypsodont teeth, and reduction in the number and size of the premolars. In this species, P² and P₂ are lacking (Webb, 1969). Unlike later species of *Megatylopus*, *M. primaevus* does not have fused P₃ roots.

Referred Specimens – **North Shore** (Kh-106): UNSM 94235, maxillary fragment with L M^{1-3} ; 9506-89, R dentary fragment with R M_{2-3} ; 9539-89, L M_3 .

Megatylopus sp.

Description – Similar to specimens described by Leite (1990), but difficult to determine species based on specimens available.

Discussion – UNSM specimens identified by Michael Voorhies and included in the faunal list by Voorhies (1990). Like *Megatylopus* cf. *M. primaevus*, this camel is very large and has hypsodont teeth. The teeth of the Cambridge specimens are larger than the *Megatylopus* cf. *M. primaevus* from the North Shore locality, but also smaller than *Megatylopus? cochrani* from the early Pliocene of Nebraska (Voorhies and Corner, 1986).

Referred specimens – **Cambridge** (Ft-40): UNSM 1250-47, L maxilla with P^4 – M^2 ; 707-48, R M_3 ; 635-48, R M^2 .

ALFORJAS Harrison, 1979

Alforjas sp.

Description – Very similar to description in Harrison (1979) but limited specimens make identification to species level difficult.

Discussion – Identified by Michael Voorhies and included in the faunal list by Voorhies (1990). *Alforjas* is a camelid intermediate in size between *Hemiauchenia* and

Megatylopus. Cheek teeth of *Alforjas* are more hypsodont than any lamine but *Camelops*. I³ and C¹/C₁ are recurved and laterally compressed. The I₁₋₃ are more broadly spatulate than in *Hemiauchenia*. The P¹/P₁ are very small and single rooted in these specimens.

Referred specimens – **Cambridge** (Ft-40): UNSM 1252-47A, L M_x; 1252-47B, L M₃.

PROCAMELUS Leidy, 1858

Procamelus grandis (Gregory, 1939)

Holotype – UCMP 32864, skull and dentary, from the Big Spring Canyon, Bennett County, South Dakota.

Description – Holotype described thoroughly in Gregory (1942).

Discussion – UNSM specimens identified by Michael Voorhies and included in faunal list as *Procamelus* sp. by Rudnick (1994). *Procamelus grandis* is a large species of *Procamelus* with slender, compressed, bladelike, caniniform teeth and thin anterior premolars. It is considerably larger than *Procamelus occidentalis*. Diastemata between caniniform teeth are of variable length, but greater than in *Procamelus robustus*. P¹/P₁ is single-rooted. Teeth are higher-crowned compared to others in the genus.

Referred specimens – **Pratt Slide** (Bw-123): UNSM 5018-89A, M₃ heel; 5024-89B, tooth fragment; 5024-89C, R M²; 5030-89, tooth fragment.

HEMIAUCHENIA Gervais and Ameghino, 1880

Hemiauchenia cf. *H. vera* (Matthew, 1909)

Holotype - AMNH 2673, the horizontal ramus of the right jaw with P₄-M₃ and the alveoli for P₃ and P₁, from near Long Island, Phillips County, Kansas.

Description – Holotype described thoroughly in Breyer (1977).

Discussion – UNSM specimens identified by Michael Voorhies and included in the faunal list by Voorhies (1990). The mandibular diastema in *Hemiauchenia vera* (approximately 35 mm) is shorter than in *Hemiauchenia blancoensis* (approximately 50 mm) or *Hemiauchenia macrocephala* (approximately 60 mm).

Referred specimens – **Cambridge** (Ft-40): UNSM 672-48, L M₃; 1405-47, R dentary fragment with M₃; 807-47, L maxilla with M¹⁻² and M³ emerging.

Hemiauchenia blancoensis (Meade, 1945)

Holotype – TMM 31181-126, a partial lower jaw with P₄-M₃, from Mount Blanco, Crosby County, Texas.

Description – Holotype described in Meade (1945).

Discussion - UNSM specimens were identified and described thoroughly in Breyer (1977). The occlusal length of the tooth row is longer than in species of *Hemiauchenia macrocephala*. The mandibular diastema is shorter than in *H. macrocephala* and longer than in *Hemiauchenia vera*. The canine is present in *H. blancoensis* and is located right after the I₃. The P₁ is caniniform and is separated from the canine by a short diastema. The P₂ is absent and the P₃ can be either present or absent but has two roots when present.

Referred specimens – **Broadwater** (Mo-5): UNSM 125709, L M₂₋₃; 125742, L M³; 125830, R M₃; 125846, L M²⁻³; 125847, R M₃; 125882, L M₃.

GIGANTOCAMELUS Barbour and Schultz, 1939

Gigantocamelus spatulus (Cope, 1893)

Holotype – not numbered by Cope or Meade.

Description – UNSM collection described as *Gigantocamelus fricki* in Barbour and Schultz (1939) and synonymized with *Plianchenia spatula* in Meade (1945) and assigned to *Gigantocamelus statulus*.

Discussion – UNSM specimens identified by Michael Voorhies and included in the faunal list for Big Springs by Voorhies (1987a). Cheek teeth are more hyposodont than in *Megatylopus*. I³ is rarely present and could be vestigial. C¹/C₁ rounded and very large. In contrast to *Titanotylopus*, the chin is very blunt. *Gigantocamelus spatulus* is also distinguished from *Titanotylopus* by the presence of a P₁ and a longer I₃-C₁ diastema (Meade, 1945). A P₁ is present in all of the specimens in the UNSM collections in which the portion of the mandible above the mental foramen is preserved.

Referred specimens – **Lisco** (Gd-12): UNSM 18409-39, L M^x; 9913-38, L M₃; 11690-38, L M²; 379-41, R M^x; 133010, R M₃. **Big Springs** (Ap-103): UNSM 27533, L M₂; 27536, L M₂; 27539, L M₃; 27542, L M₁; 27553, L M₃.

TITANOTYLOPUS Barbour and Schultz, 1934

Titanotylopus nebraskensis (Barbour and Schultz, 1934)

Holotype – UNSM 2606, right mandibular ramus with symphysis and I₁ – M₃, from Red Cloud, Webster County, Nebraska.

Description – Holotype described in Barbour and Schultz (1934) and expanded upon in Breyer (1976).

Discussion – UNSM specimens in Big Springs identified by Michael Voorhies and included in the faunal list by Voorhies (1987a). Broadwater specimens identified by Michael Voorhies and R. George Corner. Distinguished from other *Titanotylopus* species by the absence of a P₁, a shorter C-P₃ diastema and a longer mandibular symphysis projecting forward of the canines. It has a brachydont dentition and nonspatulate incisors, unlike other *Titanotylopus* species and *Gigantocamelus spatulus*. The p₃ is double rooted and more reduced than in *Megatylopus*.

Referred specimens – **Broadwater** (Mo-5): UNSM 89118, R M₃; 89123, L P⁴.
Big Springs (Ap-103): UNSM 27650, R M₃; 46878, R M³; 46879, R M²; 46880, L M³; 2213-94, R M₃.

CAMELOPS Leidy, 1854

Camelops sp.

Description – Similar to species in the description by Leidy (1854) but number of specimens makes determination of species difficult.

Discussion – UNSM specimens identified by Michael Voorhies and included in the faunal list by Barbour and Schultz (1937) and Schultz and Stout (1945). *Camelops* is the largest of the lamine camels with exception of *Blancocamelus*. It has lower molars with anteroexternal stylids that are stronger than in *Alforjas*, but weaker than in *Hemiauchenia*. Teeth are hypsodont. The limbs are long and stocky. Specimens from Broadwater are larger than *Camelops hesternus* from the Pleistocene of Nebraska (Hintlian, 1975).

Referred specimens – **Broadwater** (Mo-5): UNSM 1072-40, L M²; 4935-38, L M₃.

Family PALAEOMERYCIDAE Lydekker, 1883

CRANIOCERAS Matthew, 1918

Cranioceras unicornis (Matthew, 1918)

Holotype- AMNH 17343, late Clarendonian of Nebraska

Description – Holotype described thoroughly in Frick (1937) and Webb (1969).

Discussion – UNSM specimens identified by Michael Voorhies and included in faunal list as *Cranioceras mefferdi* by Rudnick (1994). Frick (1937) identified *Cranioceras mefferdi* from a single astragalus from Pratt Slide, but *C. mefferdi* is now considered a synonym of *Cranioceras unicornis* (Prothero and Lister, 2007). *Cranioceras unicornis* is distinguished from the only other accepted species, *Cranioceras teres*, based on size. *Cranioceras unicornis* is much larger than *C. teres*. The diastema of *C. unicornis* is short to moderate length and the premolar row is shortened with the anterior

fossette on P₄ open. *Cranioceras unicornis* has brachydont to mesodont molars. The Pratt Slide specimens look identical to the specimens in the faunal list of Blue Jay Quarry (Voorhies, 1990).

Referred specimens – **Pratt Slide** (Bw-123): UNSM 133000, R M²; 133001, L M¹; 133007, L M_x; 133008, L M_x; 133009, fragment.

Family TAYASSUIDAE Palmer, 1897

PROSTHENNOPS Gidley, 1904

Prosthennops sp.

Description – Generically described in Schultz and Martin (1975).

Discussion – UNSM specimens described by Michael Voorhies and included in faunal list by Rudnick (1994). The cheek teeth are bunodont and the P²/P₂ are not molariform. Pratt Slide specimens are slightly smaller than *Prosthennops serus* specimens from the faunal lists of the Cambridge and Lemoyne localities from the Hemphillian (Voorhies, 1990) and are larger than either *Prosthennops niobrarensis* or *Prosthennops xiphodonticus* from earlier in the Cenozoic. Specimens have very similar dentition to *Platygonus* sp. from the Blancan, but are much smaller in size.

Referred specimens – **Pratt Slide** (Bw-123): UNSM 133002, P⁴; 133003, very worn and broken M_x; 133004, P₂; 133006, M^x.

PLATYGONUS Leconte, 1848

Platygonus sp.

Description – Similar to description of *Platygonus compressus* from LeConte (1848).

Discussion – UNSM specimens identified by Michael Voorhies and included in a faunal list by Schultz and Stout (1945). Specimens have bunodont teeth with moderate to complete reduction of posterior cusps of premolars and large tusk-like canines.

Broadwater and Big Springs specimens are smaller than *Platygonus compressus* from the Pleistocene of Nebraska and larger than the *Platygonus* sp. from the latest Hemphillian in the Santee local fauna (Voorhies, 1990).

Referred specimens – **Broadwater** (Mo-5): 53643, R M_x; 53645, R dentary with P₂ – M₂ and M₃ erupting; 53651, R dentary with P₃ – M₁; 53653, L dentary with P₂ – M₃.
Big Springs (Ap-103): 51643, R dentary with P₃ – M₁ and M₂ fragment; 54937, L M₃; 3021-98, R dentary with P₄ – M₂.

Stable Isotope Notation

Isotopic results are expressed in standard δ -notation: $X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$, where X is the $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ value, and $R = {}^{13}\text{C} / {}^{12}\text{C}$ or ${}^{18}\text{O} / {}^{16}\text{O}$, respectively. The $\delta^{13}\text{C}$ 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.

Carbon Isotopes in Mammalian Diet

Carbon isotope compositions of fossil teeth are useful in paleodiet studies. This is because the three different photosynthetic pathways used by plants: C₃, C₄, and crassulacean acid metabolism (CAM) impart different ¹³C/¹²C ratios. These ratios are ultimately reflected in chemical composition of body fluids and tissues of the animals that eat the different types of plants. Tropical, warm growing-season grasses and sedges using the C₄, or Hatch-Slack, photosynthetic pathway are enriched in ¹³C. These plants have a mean δ¹³C value of -13‰ and generally range from -9‰ to -19‰ (O'Leary, 1988). Conversely, C₃, or Calvin cycle, plants, which include most trees and shrubs, as well as cool growing-season grasses, are ¹³C – depleted. C₃ plants have a mean δ¹³C value of -27‰ and typically range from -22‰ to -35‰ (O'Leary, 1988). The third pathway, the CAM pathway, is characteristic of succulents and generally yields values ranging those of C₃ and C₄ plants (O'Leary, 1988; Ehleringer et al., 1991). CAM photosynthesis is usually found in more restricted arid habitats. Since CAM plants are generally not widespread (Ehleringer et al., 1991), they are not considered further.

Mammalian herbivore tooth enamel reflects the isotopic ratio of the plants ingested (DeNiro and Epstein, 1978; Vogel, 1978). Taxa that feed on grasses and sedges are considered grazers, those taxa that feed on trees and shrubs are browsers, and the taxa that feed on a mixture of grasses, sedges, trees, and shrubs are considered mixed feeders. Studies utilizing differences in the carbon isotope values in mammals generally focus on ecosystems that have a mixture of C₃ and C₄ plants available which enables taxa to be distinguished on the basis of the predominant forage included in their diet (Vogel, 1978; MacFadden and Cerling, 1996; Cerling et al., 1997; Cerling et al., 1998; Koch, 1998;

MacFadden et al., 1999). These studies are geographically restricted in scope because modern C₄ plants are confined to lower latitudes. At higher latitudes (i.e., above 43°N in North America), plants almost entirely utilize the C₃ photosynthetic pathway (Teeri and Stowe, 1976). While this study partially focuses on C₄ environments, half of the localities are C₃ exclusive because they are before the expansion of C₄ grasslands. Some variability of carbon isotope values exists even within a completely C₃ habitat. Variation in light intensity, temperature, nutrient availability, and water stress affect δ¹³C values in C₃ plants (O'Leary et al., 1992; Koch, 1998). C₃ plants exhibit the lowest δ¹³C values in closed, forested habitats due to the recycling of ¹³C-depleted CO₂ under the canopy (Vogel, 1978; van der Merwe and Medina 1991). and from decreased irradiance below the canopy (Ehleringer et al., 1986; Heaton, 1999) called the “canopy effect”. Relatively high δ¹³C values are characteristic of more open, drier habitats (O'Leary et al., 1992; Koch, 1998; Cerling and Harris, 1999; Feranec and MacFadden, 2006; Secord et al., 2008).

Plant carbon ingested by herbivores is incorporated into the mineralized tissues of the animal. In mammals, these tissues have a mineralogy similar to hydroxyapatite [Ca₅(PO₄)₃(OH)] with substitutions of CO₃ for PO₄ and OH (Passey et al., 2005). The CO₃ component of tooth enamel therefore assumes a δ¹³C value that reflects the carbon isotope composition of the ingested plants. However, both metabolism and biomineralization fractionate ingested carbon so that bioapatites are enriched in ¹³C relative to the bulk diet. This enrichment factor is 13.3 ± 0.3‰ (1 SD) for non-ruminant and 14.6 ± 0.3‰ for ruminant ungulates (Passey et al., 2005).

Oxygen Isotopes in Tooth Enamel

Oxygen isotope compositions of mammalian enamel depend on the $\delta^{18}\text{O}$ value of ingested water, the consistent fractionation of oxygen isotopes between body water and the tooth enamel, and the metabolism of the particular taxon (Land et al., 1980; Longinelli, 1984; Luz and Kolodny, 1985; Kohn, 1996; Kohn et al., 1996; Kohn et al., 1998). Mammalian herbivores ingest water through drinking or consuming plants. The isotopic composition of water is affected by climatic factors such as temperature, amount of precipitation, and relative humidity. Warmer temperatures result in more positive $\delta^{18}\text{O}$ values in meteoric waters because the lighter isotope (^{16}O) is preferentially evaporated, which are reflected in the tooth enamel, while lower temperatures result in lower $\delta^{18}\text{O}$ values (Figure 2) (Dansgaard, 1964; Rozanski et al., 1992; Fricke and O'Neil, 1996; Kohn and Welker, 2005).

Oxygen isotope compositions of mammalian tooth enamel can also vary between taxa occupying similar environments because of variations in the relative proportion of drinking water and plant water (Balasse et al., 2003; Levin et al., 2006). Species that derive a significant proportion of water from leaves and / or live in arid regions (i.e., $\delta^{18}\text{O}_{\text{enamel}}$ values increase with aridity) should be ^{18}O -enriched compared to those that are obligate drinkers (i.e., $\delta^{18}\text{O}_{\text{enamel}}$ values track meteoric water) in the same local area (Balasse et al., 2003; Levin et al., 2006). In addition, aquatic or semi-aquatic mammals such as hippopotami generally have lower $\delta^{18}\text{O}$ values than associated terrestrial mammals (Clementz et al. 2008).

Additionally, the photosynthetic pathway of plants eaten by herbivores can influence the isotopic composition of its water. There is a tendency for leaf water of C₄ grasses to be more ¹⁸O-enriched than the leaf water of C₃ grasses (Helliker and Ehleringer, 2002).

Additionally, enrichment in δ¹⁸O values in the leaves is more pronounced in warmer and more arid conditions (Yakir et al., 1990; Yakir, 1992). This enrichment is especially the case when comparing C₃ to C₄ plants. Leaf water differences between C₃ and C₄ plants are significant under low humidity growth conditions (Helliker and Ehleringer, 2002).

While C₄ plants always have higher δ¹⁸O values compared to C₃ plants, the difference diminishes from about an average ¹⁸O enrichment of 5‰ at low humidity to approximately 1‰ at high humidity (Helliker and Ehleringer, 2002).

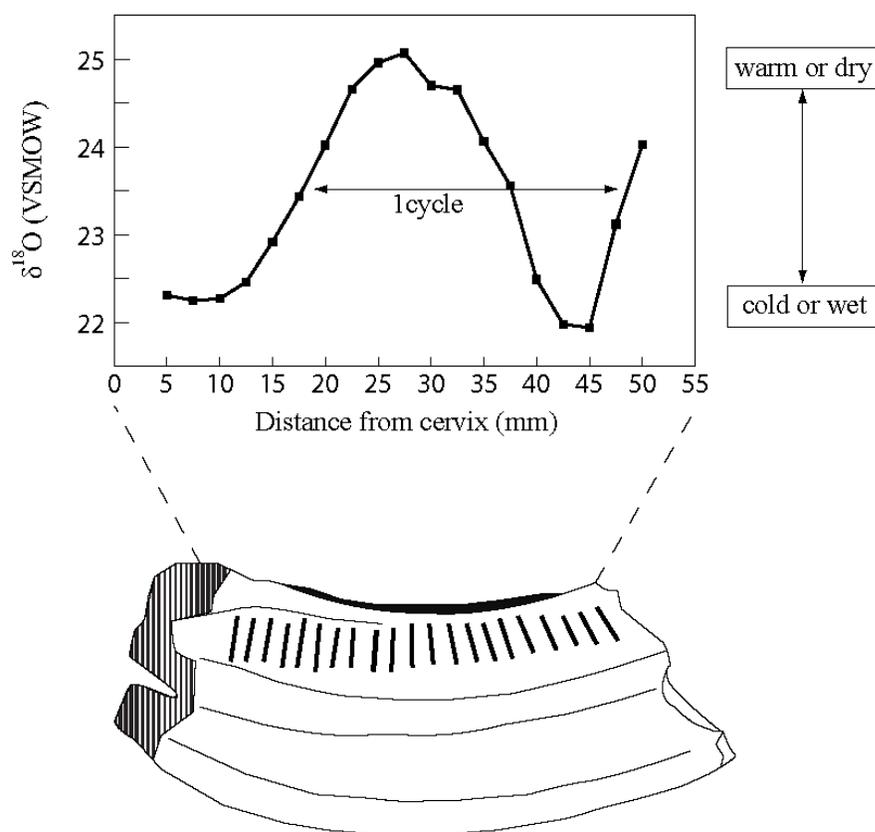


Figure 2: Example of serial sampling of enamel along a tooth, and intra-tooth variation in oxygen isotope ratios (δ¹⁸O) of enamel bioapatite.

Body size and metabolism can also affect $\delta^{18}\text{O}$ values. The largest fossil taxa are suggested to be used for paleoclimate reconstruction because potential errors are smallest at large body sizes and low metabolism (Longinelli, 1984; Bryant and Froelich, 1995). This is because the amount of oxygen derived from metabolism of food and from O_2 uptake decreases at larger body size, while the proportion of water taken up as a liquid increases (Bryant and Froelich, 1995). The problems with estimating the isotopic composition of atmospheric oxygen ($\delta^{18}\text{O}_\text{A}$) and the isotopic composition of metabolic oxygen incorporated into the body ($\delta^{18}\text{O}_\text{F}$) are then minimized with larger body sizes (Bryant and Froelich, 1995). Because the proportion of oxygen taken up as liquid water increases while the food requirement decreases, the proportion of surficial drinking water reflected in the isotopic composition of water will increase with increasing body size. The $\delta^{18}\text{O}$ of surficial drinking water reflected in the ingested water of the taxon is the most direct archive for paleoclimate reconstruction (Bryant and Froelich, 1995). All taxa analyzed at the six fossil localities are large and considered to have lower metabolic rates.

METHODS

Sample Selection

Samples of tooth enamel from 101 specimens collected from six localities in Nebraska were bulk sampled. These include specimens from the North Shore, Pratt Slide, Cambridge, Lisco, Broadwater, and Big Springs localities, which span the late Clarendonian to late Blancan land-mammal ages (Figure 1). Preference was given to

sampling third molars and premolars ($P_2 - P_4$) since these teeth are among the last ones to develop, mineralize, and erupt in mammals (Hillson, 2005), avoiding a potential weaning signal. When necessary, these samples were supplemented by sampling second and first molars. Isolated teeth were chosen, particularly those that would be less critical to further study and were in good physical condition with no carbonate etching.

For serial sampling, a total of 124 isotopic samples were analyzed from six specimens from the Cambridge (medial Hemphillian) and Big Springs (late Blancan) localities in Nebraska. *Neohipparion eurystyle* was sampled from the Cambridge locality and *Equus simplicidens* was sampled from the Big Springs locality. Upper third molars were the only teeth used for serial sampling.

Sampling and Pretreatment

The general method for stable isotope sampling of tooth enamel followed Koch et al. (1997). For the bulk and serial sampling, 3-4 mg of pristine enamel powder was drilled from the tooth along a non-occlusal surface parallel to the growth axis using a 1 mm diamond bit and a variable speed dental drill. For serial sampling, samples were drilled parallel to perikymata when visible. A sample was taken every 2 mm for *N. eurystyle*, which had lower-crowned teeth, and every 2.5 mm for *E. simplicidens*, which had higher-crowned teeth, resulting in 17-25 samples per tooth. The position of each groove is recorded in millimeters from the cervix (Figure 2).

The powder was collected and treated with 2-3% reagent grade NaOCl (sodium hypochlorite) for 24 hours to remove organic matter. The samples were rinsed five times

with distilled water and dried. Nonstructural carbonates were removed by soaking in 1 M buffered acetic acid for 24 hours. This was followed by rinsing and drying. Our protocol differs from Koch et al. (1997) at this point in that samples were not lyophilized.

Isotope Analysis

Samples were reacted with phosphoric acid for 17 minutes at $77^{\circ}\pm 1^{\circ}$ °C in a Finnigan MAT Kiel IV preparation device at the University of Michigan Stable Isotope Laboratory (UMSIL). Isotopic ratios of the resulting CO₂ were measured with a Finnigan MAT 253 triple collector isotope ratio mass spectrometer. Analytical precision at UMSIL is better than $\pm 0.1\text{‰}$ (1 SD) for both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, based on international standards for carbonate (NBS-18, NBS-19) (Lora Wingate – personal communication). Intra-lab enamel standards (LOX, from African elephant; MES-1, from fossil mammoth enamel from New Mexico) were used to monitor variance among batches. Mean values and variances were: $\delta^{18}\text{O} = 32.07 \pm 0.04\text{‰}$ and $\delta^{13}\text{C} = -5.66 \pm 0.01\text{‰}$ (95% confidence, n = 29) for LOX and $\delta^{18}\text{O} = 23.30 \pm 0.07\text{‰}$ and $\delta^{13}\text{C} = -9.67 \pm 0.01\text{‰}$ (n = 19) for MES-1.

I performed a pairwise comparison of all genera represented by two or more isotope values in each locality using analysis of variance tests (ANOVA). Fisher's LSD test indicates that many taxa have significantly different mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (Table 3). In addition, I applied Tukey's post hoc test, which adjusts for number of pairs.

Predicting Carbon Isotope Values for Late Neogene Mammals

I developed a model to predict expected $\delta^{13}\text{C}$ values in herbivores from a variety of late Neogene habitats. Far more $\delta^{13}\text{C}$ values have been published for extant plants than for extant mammals. Thus, I used data from extant plants. I normalized values for modern vegetation to parameters for the late Neogene of Nebraska. Factors that were considered were (1) the effects of latitude on $\delta^{13}\text{C}$ values in vegetation; (2) diet-enamel enrichment; and (3) changes in the composition of atmospheric CO_2 ($\delta^{13}\text{C}_A$) between the late Neogene and present.

A mean increase of $0.3\text{‰} / 10^\circ$ latitude in $\delta^{13}\text{C}$ values occurs in leaves receiving the same amount of light and water (calculation by Secord et al. 2008; data from Körner et al. 1991). To compensate, I normalized modern plant data to 42°N , the approximate latitude of Nebraska. This allowed me to make cutoffs for various habitats including: closed canopy, open woodland, C_3 grassland, and C_4 grassland (Figure 3). The large gap between $\delta^{13}\text{C}$ values from C_3 and C_4 grasslands are considered a mixture of plants with these different photosynthetic pathways.

As mentioned earlier, the enrichment factor is $13.3 \pm 0.3\text{‰}$ (1 SD) for non-ruminant and $14.6 \pm 0.3\text{‰}$ for ruminant ungulates (Passey et al., 2005). This study looks at both ruminants and non-ruminant ungulates, so an averaged enrichment factor of approximately 14.0‰ is used, as suggested by Cerling and Harris (1999) in an analysis of ungulates. Changes in $\delta^{13}\text{C}_A$ can be estimated from the tests of fossil foraminifers because they incorporate dissolved carbon with predictable fractionation from vital effects (Passey et al. 2002). I used data compiled by Zachos et al. (2001) from two

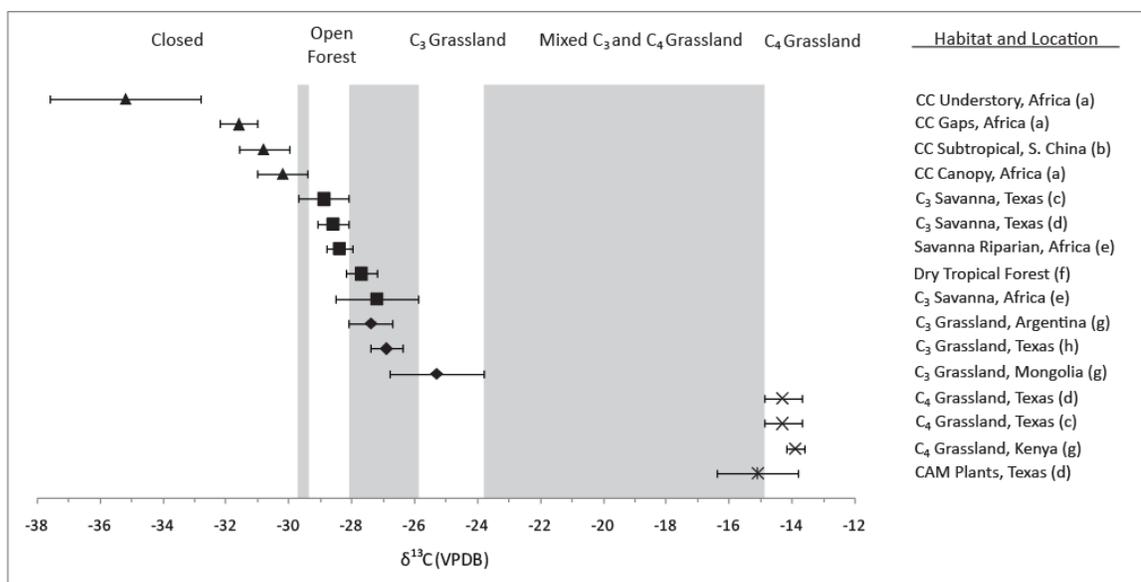


Figure 3: Predicted cutoffs for various habitats. Predictions based on $\delta^{13}\text{C}$ values from modern floras, normalized to 42°N latitude. Gray areas indicate overlap in $\delta^{13}\text{C}$ values for habitats. Error bars show 95% confidence of mean (± 1.96 SE). CC = closed canopy. Data sources: a, Cerling et al. (2004); b, Ehleringer et al. (1987); c, Boutton et al. (1998); d, Jessup et al. (2003); e, Codron et al. (2005); f, Mooney et al. (1989); g, Cerling and Harris (1999).

lineages of benthic foraminifers, adjusted for vital effects, to calculate changes in $\delta^{13}\text{C}_A$. The mean foraminifer value in the Blancan is only $\sim 0.3\text{‰}$ more negative than the mean pre-industrial value for the last 1000 years. The medial Hemphillian and the late Clarendonian had $\delta^{13}\text{C}_A$ values that were $.3\text{‰}$ and $.9\text{‰}$ more positive than the pre-industrial value, respectively. In addition, there is an increase of $\sim 1.5\text{‰}$ in the $\delta^{13}\text{C}_A$ values caused by industrialization over the last two centuries (Friedli et al. 1986). As an example, these effects taken together imply that the $\delta^{13}\text{C}_A$ values at the time of the Blancan were $\sim 1.2\text{‰}$ more positive than today. These two factors lead to an increase of $\sim 15.2\text{‰}$ for each of the different habitats (Figure 4).

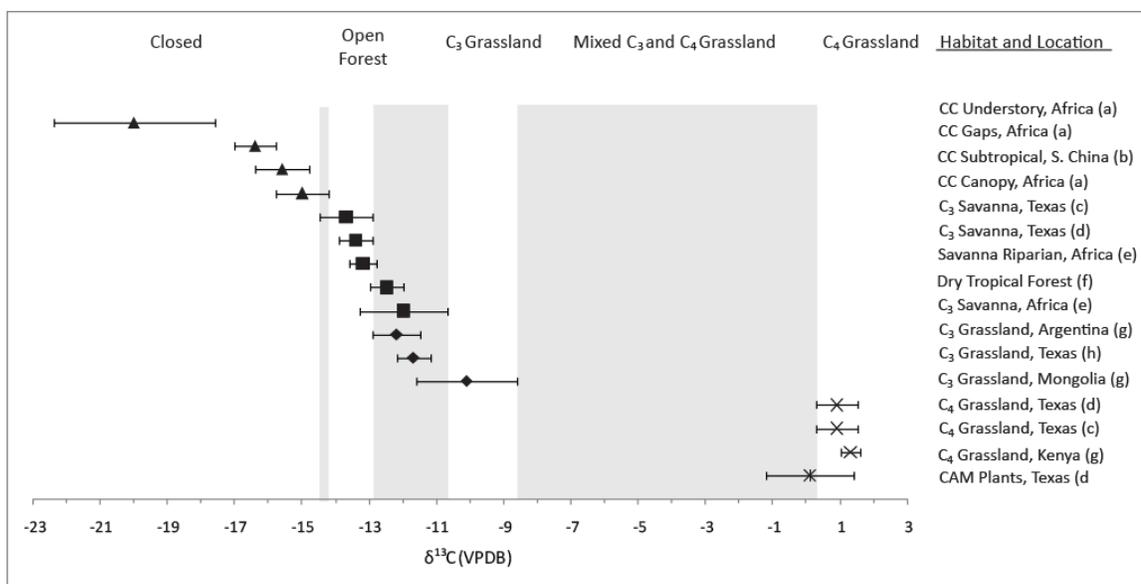


Figure 4: Predicted cutoffs for tooth enamel from various habitats in the Blancan. Predictions are based on $\delta^{13}\text{C}$ values from modern floras, normalized to 42°N latitude, corrected for a 1.3‰ difference in atmospheric $\delta^{13}\text{C}$ values, and a diet-enamel enrichment of 14‰ . Error bars show 95% confidence of mean (± 1.96 SE). See Figure 3 for abbreviations.

RESULTS

Bulk Sampling

The eighteen samples from the North Shore locality display the most positive mean $\delta^{13}\text{C}$ values amongst Miocene localities at $-9.4\text{‰} \pm 0.3\text{‰}$ (Table 1). The twenty samples from the Pratt Slide locality display the lowest mean $\delta^{13}\text{C}$ value amongst Miocene localities at $-11.8\text{‰} \pm 0.4\text{‰}$. The 21 samples from the Cambridge locality display a mean $\delta^{13}\text{C}$ value of $-9.9\text{‰} \pm .4\text{‰}$. The five samples from the Lisco locality display the highest mean $\delta^{13}\text{C}$ value for all Pliocene localities at $-3.1\text{‰} \pm 1.0\text{‰}$ (Figure 5). The sixteen samples from the Broadwater locality display the lowest mean $\delta^{13}\text{C}$ value among Pliocene localities at $-8.1\text{‰} \pm 1.2\text{‰}$. The 21 samples from the Big Springs locality display a mean $\delta^{13}\text{C}$ value at $-5.0\text{‰} \pm 1.6\text{‰}$.

The mean $\delta^{18}\text{O}$ value for the eighteen samples at North Shore is $25.9\text{‰} \pm 0.8\text{‰}$ (Table 1, Figure 5). Similar to the mean $\delta^{13}\text{C}$ value, the mean $\delta^{18}\text{O}$ value for the twenty samples at Pratt Slide is the lowest among Miocene localities at $25.7\text{‰} \pm 0.9\text{‰}$. The mean $\delta^{18}\text{O}$ value for the 21 samples at Cambridge is the highest amongst Miocene localities at $26.8\text{‰} \pm .7\text{‰}$. The mean $\delta^{18}\text{O}$ value for the five samples at Lisco is $22.9\text{‰} \pm .4\text{‰}$ with a range from 22.4‰ to 23.5‰ . Similar to the $\delta^{13}\text{C}$ value, the mean $\delta^{18}\text{O}$ value for the sixteen samples at Broadwater is the highest among Pliocene localities at $22.6\text{‰} \pm 1.1\text{‰}$. The mean $\delta^{18}\text{O}$ value for the 21 samples at Big Springs is the highest among Pliocene localities at $23.3\text{‰} \pm 1.0\text{‰}$.

Table 1: Descriptive statistics for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from the 6 Nebraskan localities.

	$\delta^{13}\text{C}$ (VPDB)					
	North Shore	Pratt Slide	Cambridge	Lisco	Broadwater	Big Springs
<i>n</i>	18	20	21	5	16	21
Mean	-9.4	-11.8	-9.9	-3.1	-8.1	-5.0
Minimum	-10.9	-14.5	-11.8	-4.5	-11.3	-11.7
Maximum	-8.4	-10.2	-8.0	-2.1	-3.8	0.8
Range	2.5	4.4	3.8	2.4	7.5	12.5
SD	0.74	0.95	0.94	1.09	2.36	3.67
SE	0.17	0.21	0.21	0.49	0.59	0.80
	$\delta^{18}\text{O}$ (VSMOW)					
	North Shore	Pratt Slide	Cambridge	Lisco	Broadwater	Big Springs
<i>n</i>	18	20	21	5	16	21
Mean	25.9	25.7	26.8	22.9	22.4	23.3
Minimum	22.6	22.0	24.1	22.4	17.7	19.5
Maximum	29.7	28.6	30.0	23.5	27.5	27.2
Range	7.1	6.6	5.9	1.1	9.8	7.7
SD	1.75	2.02	1.63	0.49	2.21	2.37
SE	0.41	0.45	0.36	0.22	0.55	0.52

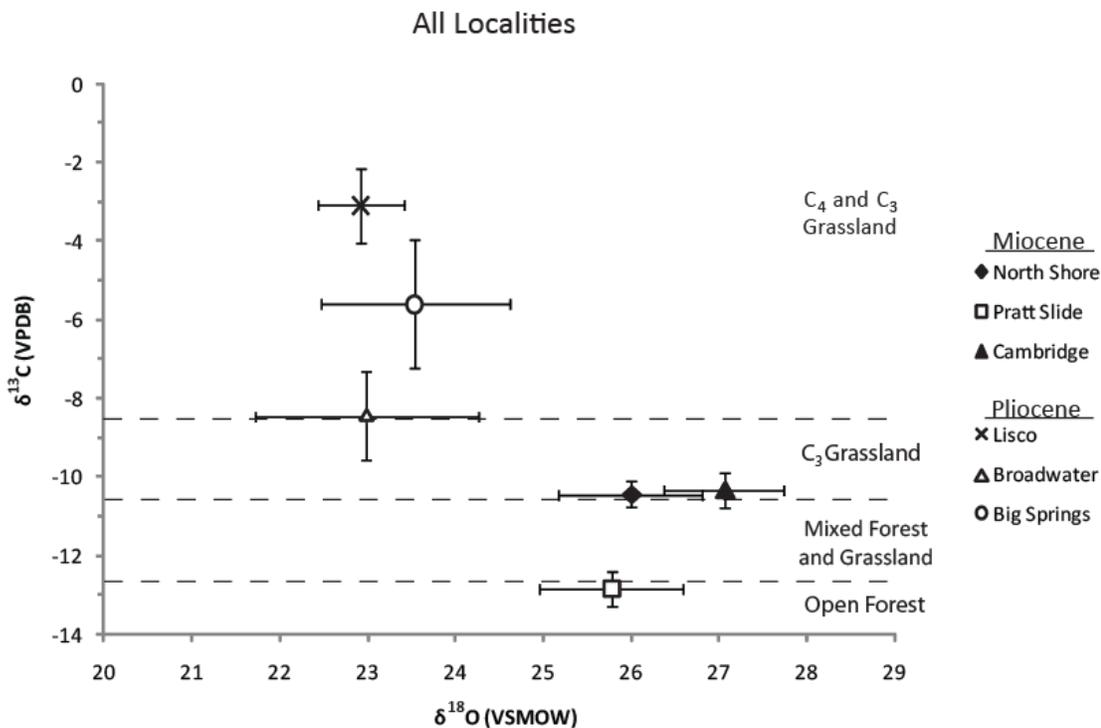


Figure 5: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, normalized for Blancan $\delta^{13}\text{C}_A$, from all Nebraskan localities with interpreted habitats (Figure 4). Symbols represent the mean value; error bars represent 95% confidence (± 1.96 SE).

North Shore Locality

Serbelodon cf. *S. barbourensis* is significantly lower than both *Teleoceras major* and *Cormohipparion occidentale* using standard t-tests (Table 2A, Figure 6). Within the taxa present, *C. occidentale* has the most positive mean $\delta^{13}\text{C}$ value at $-9.0\text{‰} \pm 0.4\text{‰}$ and a range from -9.3‰ to -8.4‰ for five samples (Appendix A). The taxon displaying the lowest mean $\delta^{13}\text{C}$ value is cf. *S. barbourensis*, which has a mean carbon isotope value of $-10.5\text{‰} \pm .6\text{‰}$ with a range from -10.8‰ to -10.2‰ for two samples.

Serbelodon cf. *S. barbourensis* has significantly lower $\delta^{18}\text{O}$ values than either *Megatylopus* cf. *M. primaevus* or *Cormohipparion occidentale* (Table 2B). Of the taxa

present, cf. *M. primaevus* has the most positive mean $\delta^{18}\text{O}$ value at $27.4\text{‰} \pm 2.4\text{‰}$ and a range from 25.9‰ to 29.7‰ for three samples. The taxon displaying the lowest mean $\delta^{18}\text{O}$ value is cf. *S. barbourensis*, which has a mean oxygen isotope value of $23.8\text{‰} \pm 1.4\text{‰}$ and a range from 23.1‰ to 24.5‰ for two samples.

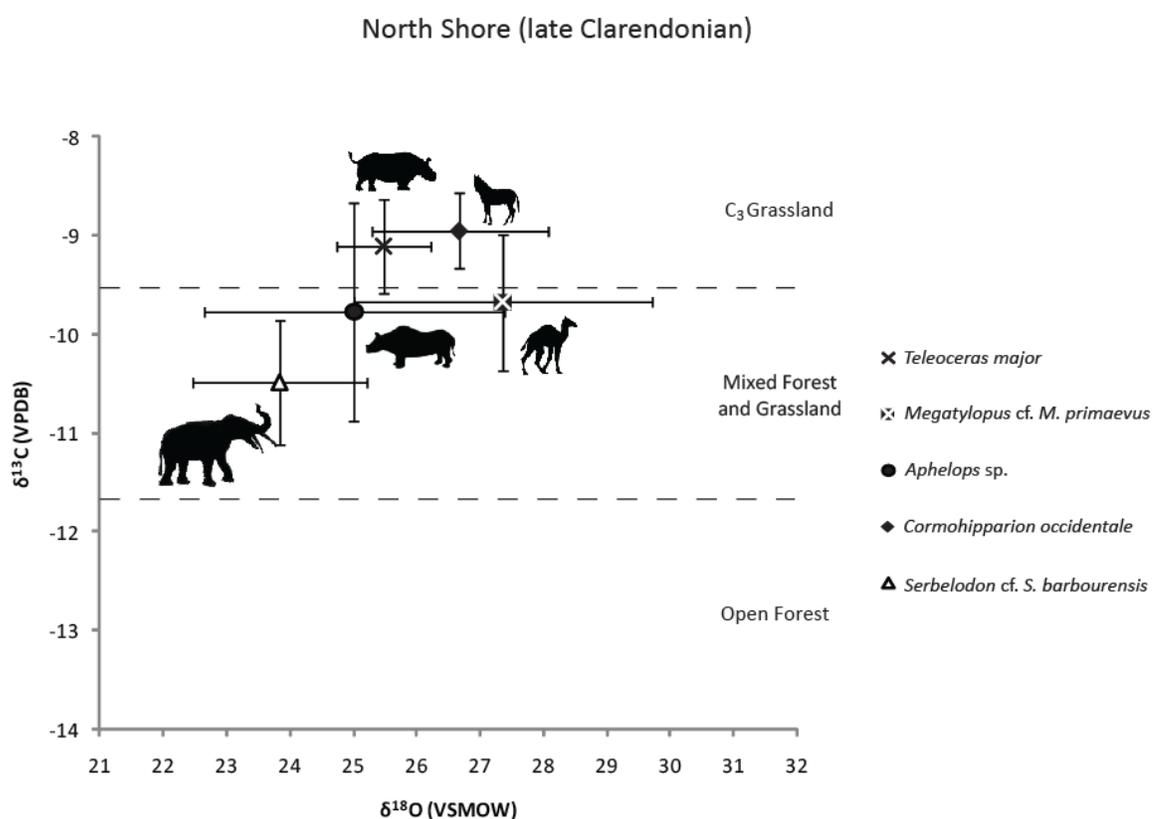


Figure 6: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from mammalian taxa at the North Shore locality with interpreted habitats. Symbols represent the mean value; error bars represent 95% confidence (± 1.96 SE).

Table 2: Matrices of pairwise probabilities of mean differences in $\delta^{13}\text{C}$ (A, C, E, G, I) and $\delta^{18}\text{O}$ (B, D, F, H, J) values among mammalian taxa in Nebraskan localities with more than one taxon. Values shown in bold indicate significance for $\alpha \leq 0.05$ using Fisher's least significance test. Pairs that were significant using Tukey's post hoc test ($\alpha \leq 0.05$) are indicated by an asterisk.

A. $\delta^{13}\text{C}$	1	2	3	4	5
North Shore					
1. <i>Aphelops</i>	1.000				
2. <i>Cormohipparion</i>	0.088	1.000			
3. <i>Megatylopus</i>	0.849	0.128	1.000		
4. <i>Serbelodon</i>	0.223	0.010	0.170	1.000	
5. <i>Teleoceras</i>	0.160	0.691	0.225	0.018	1.000

B. $\delta^{18}\text{O}$	1	2	3	4	5
North Shore					
1. <i>Aphelops</i>	1.000				
2. <i>Cormohipparion</i>	0.166	1.000			
3. <i>Megatylopus</i>	0.086	0.555	1.000		
4. <i>Serbelodon</i>	0.424	0.048	0.027	1.000	
5. <i>Teleoceras</i>	0.685	0.246	0.121	0.229	1.000

C. $\delta^{13}\text{C}$	1	2	3	4	5	6
Pratt Slide						
1. <i>Cormohipparion</i>	1.000					
2. <i>Cranioceras</i>	0.808	1.000				
3. <i>Hipparion</i>	0.260	0.257	1.000			
4. <i>Procamelus</i>	0.101	0.070	0.564	1.000		
5. <i>Prosthennops</i>	0.186	0.159	0.863	0.661	1.000	
6. <i>Teleoceras</i>	0.180	0.173	0.716	0.899	0.816	1.000

D. $\delta^{18}\text{O}$	1	2	3	4	5	6
Pratt Slide						
1. <i>Cormohipparion</i>	1.000					
2. <i>Cranioceras</i>	0.056	1.000				
3. <i>Hipparion</i>	0.513	0.145	1.000			
4. <i>Procamelus</i>	0.022	0.485	0.054	1.000		
5. <i>Prosthennops</i>	0.001*	0.000*	0.000*	0.000*	1.000	
6. <i>Teleoceras</i>	0.456	0.010	0.153	0.004*	0.003*	1.000

Table 2: Continued

E. $\delta^{13}\text{C}$	1	2	3	4	5	6	7
Cambridge							
1. <i>Alforjas</i>	1.000						
2. <i>Aphelops</i>	0.705	1.000					
3. <i>Calippus</i>	0.495	0.296	1.000				
4. <i>Hemiauchenia</i>	0.096	0.195	0.023	1.000			
5. <i>Megatylopus</i>	0.848	0.824	0.352	0.098	1.000		
6. <i>Neohipparion</i>	0.024	0.010	0.111	0.000*	0.007	1.000	
7. <i>Teleoceras</i>	0.869	0.549	0.532	0.036	0.678	0.011	1.000
F. $\delta^{18}\text{O}$	1	2	3	4	5	6	7
Cambridge							
1. <i>Alforjas</i>	1.000						
2. <i>Aphelops</i>	0.066	1.000					
3. <i>Calippus</i>	0.527	0.019	1.000				
4. <i>Hemiauchenia</i>	0.307	0.281	0.098	1.000			
5. <i>Megatylopus</i>	0.780	0.079	0.337	0.400	1.000		
6. <i>Neohipparion</i>	0.004	0.332	0.001*	0.023	0.003*	1.000	
7. <i>Teleoceras</i>	0.007	0.423	0.002*	0.039	0.006	0.854	1.000
G. $\delta^{13}\text{C}$	1	2	3	4	5		
Broadwater							
1. <i>Camelops</i>	1.000						
2. <i>Equus</i>	0.281	1.000					
3. <i>Hemiauchenia</i>	0.788	0.124	1.000				
4. <i>Platygonus</i>	0.186	0.020	0.151	1.000			
5. <i>Titanotylopus</i>	0.863	0.216	0.954	0.254	1.000		
H. $\delta^{18}\text{O}$	1	2	3	4	5		
Broadwater							
1. <i>Camelops</i>	1.000						
2. <i>Equus</i>	0.636	1.000					
3. <i>Hemiauchenia</i>	0.176	0.066	1.000				
4. <i>Platygonus</i>	0.085	0.032	0.494	1.000			
5. <i>Titanotylopus</i>	0.817	0.485	0.272	0.134	1.000		

Table 2: Continued

I. $\delta^{13}\text{C}$	1	2	3	4	5
Big Springs					
1. <i>Equus</i>	1.000				
2. <i>Gigantocamelus</i>	0.681	1.000			
3. <i>Platygonus</i>	0.001*	0.004*	1.000		
4. <i>Stegomastodon</i>	0.293	0.192	0.001*	1.000	
5. <i>Titanotylopus</i>	0.852	0.569	0.001*	0.370	1.000
J. $\delta^{18}\text{O}$	1	2	3	4	5
Big Springs					
1. <i>Equus</i>	1.000				
2. <i>Gigantocamelus</i>	0.474	1.000			
3. <i>Platygonus</i>	0.065	0.209	1.000		
4. <i>Stegomastodon</i>	0.800	0.784	0.211	1.000	
5. <i>Titanotylopus</i>	0.058	0.227	0.829	0.237	1.000

Pratt Slide Locality

Within the taxa present, *Procamelus grandis* has the most positive mean $\delta^{13}\text{C}$ value at $-11.2\text{‰} \pm 0.9\text{‰}$ and a range from -12.2‰ to -10.2‰ for four samples (Figure 7, Appendix A). The taxon displaying the lowest mean $\delta^{13}\text{C}$ value is *Cormohipparion* sp., which has a mean $\delta^{13}\text{C}$ value of $-12.6\text{‰} \pm 0.7\text{‰}$ and a range from -13.0‰ to -12.3‰ for two samples.

Within this locality, *Prosthennops* sp. shows statistically significantly lower values than all other taxa using either Fisher test or Tukey's post hoc test (Table 2D). Among the taxa present, *Procamelus grandis* has the most positive mean $\delta^{18}\text{O}$ value at $27.5\text{‰} \pm 0.8\text{‰}$ and a range from 27.0‰ to 28.6‰ for four samples. The taxon

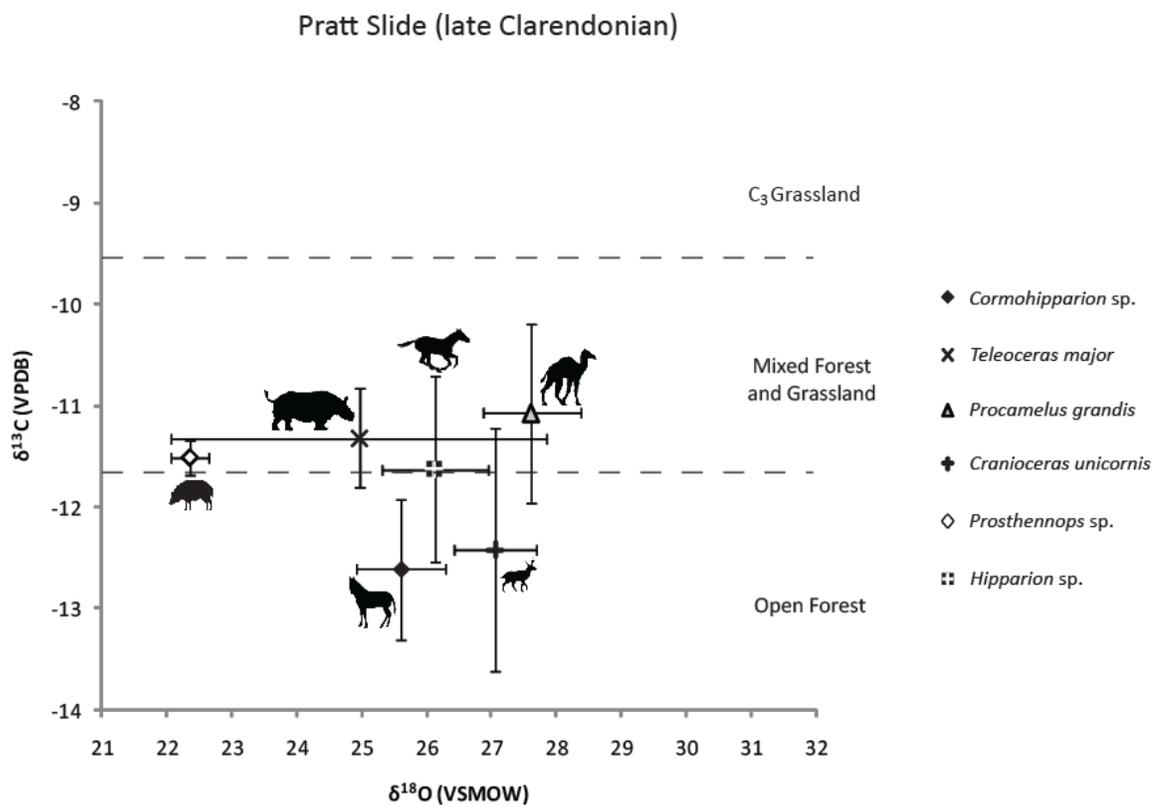


Figure 7: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from mammalian taxa at the Pratt Slide locality with interpreted habitats. Symbols represent the mean value; error bars represent 95% confidence (± 1.96 SE).

displaying the lowest mean $\delta^{18}\text{O}$ value is *Prosthennops* sp., which has a mean oxygen isotope value of $22.4\text{‰} \pm 0.3\text{‰}$ and a range from 22.0‰ to 22.7‰ for four samples.

Cambridge Locality

Within the taxa present, *N. eurystyle* has the most positive mean $\delta^{13}\text{C}$ value at $-8.7\text{‰} \pm .5\text{‰}$ and a range from -9.3‰ to -8.0‰ for five samples (Figure 8). This is significantly higher than cf. *H. vera*, which has a mean of $-11.2\text{‰} \pm .8\text{‰}$ and a range

from -11.8‰ to -10.4‰ for three samples (Table 2F). Two camelids (*Megatylopus* sp. and *Alforjas* sp.) have very similar mean $\delta^{13}\text{C}$ values (-10.2‰ and -10.1‰ respectively).

Among taxa present, *Calippus* sp. is significantly different from both *Neohipparion eurystyle* and *Teloeceras fossiger*. *Neohipparion eurystyle* is also significantly different from *Megatylopus* sp. *Calippus* sp. has the most positive mean $\delta^{18}\text{O}$ value at $29.0\text{‰} \pm 1.9\text{‰}$ and a range from 28.1‰ to 30.0‰ for two samples. The taxon displaying the lowest mean $\delta^{18}\text{O}$ value is *N. eurystyle*, which has a mean oxygen isotope value of $25.4\text{‰} \pm 1.1\text{‰}$ and a range from 24.1‰ to 27.2‰ for five samples. Similar to the $\delta^{13}\text{C}$ values, *Megatylopus* sp. and *Alforjas* sp. have very similar mean $\delta^{18}\text{O}$ values (28.1‰ and 28.3‰ respectively).

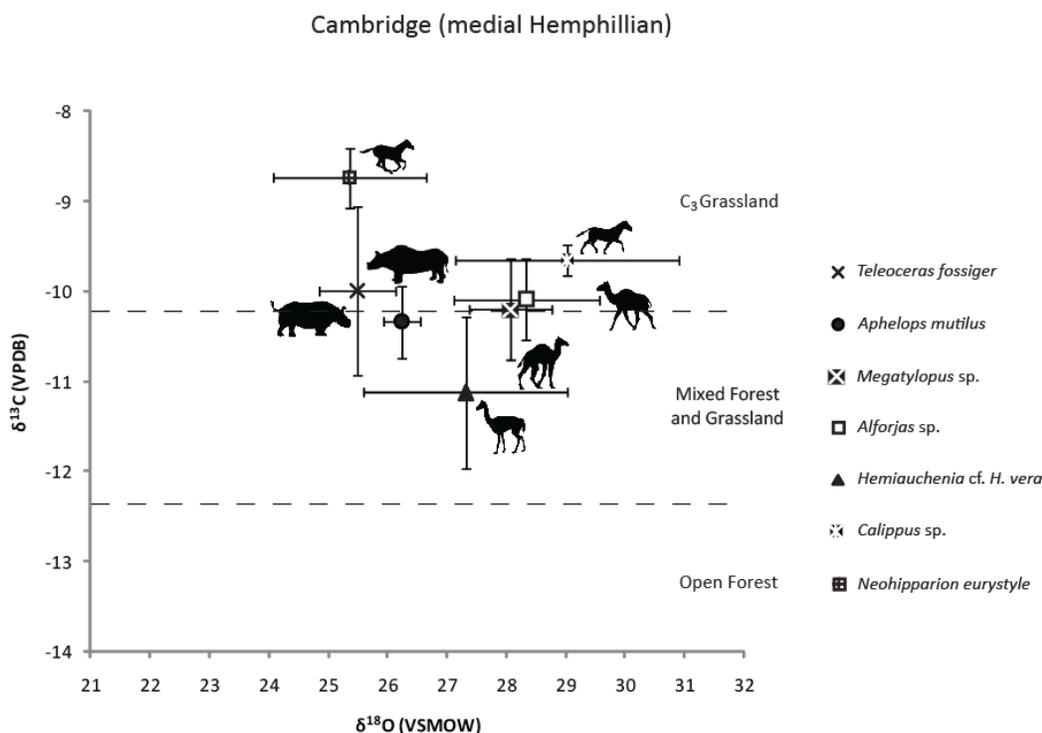


Figure 8: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from mammalian taxa at the Cambridge locality with interpreted habitats. Symbols represent the mean value; error bars represent 95% confidence (± 1.96 SE).

Lisco Locality

The only taxon represented in this locality is *Gigantocamelus spatulus*, which has a mean $\delta^{13}\text{C}$ value of $-3.1\text{‰} \pm 1.0\text{‰}$ and a range from -4.5‰ to -2.1‰ for five samples (Figure 9). The mean $\delta^{18}\text{O}$ value for *G. spatulus* is $22.9\text{‰} \pm .4\text{‰}$ with a range from 22.4‰ to 23.5‰ .

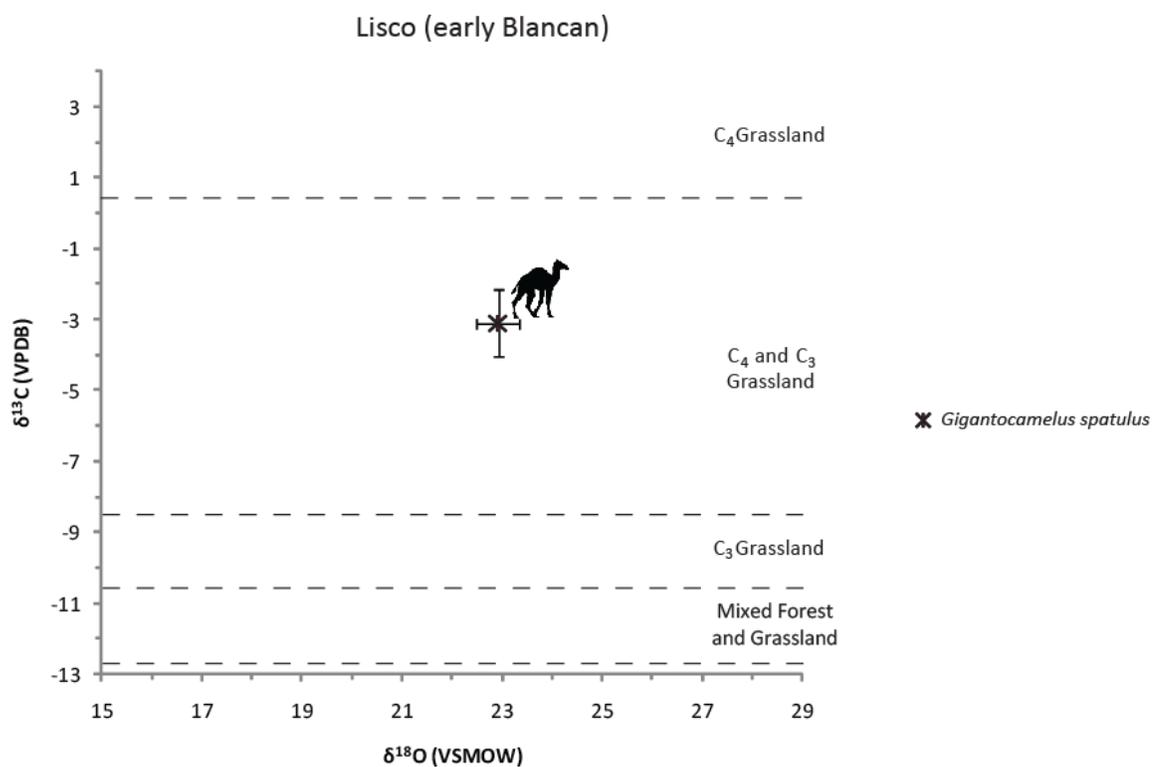


Figure 9: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from mammalian taxa at the Lisco locality with interpreted habitats (Figure 4). Symbols represent the mean value; error bars represent 95% confidence (± 1.96 SE).

Broadwater Locality

Within the taxa present, *Equus simplicidens* has the most positive mean $\delta^{13}\text{C}$ value at $-5.1\text{‰} \pm 2.7\text{‰}$ and a range from -6.5‰ to -3.8‰ for two samples (Figure 10). The taxon displaying the lowest mean $\delta^{13}\text{C}$ value is *Platygonus* sp., which has a mean value of $-10.1\text{‰} \pm 0.8\text{‰}$ and a range from -11.3‰ to -9.5‰ for four samples. Two camelids (*Titanotylopus nebraskensis* and *Camelops* sp.) have very similar $\delta^{13}\text{C}$ values (-7.9‰ and -7.5‰ respectively). *Platygonus* sp. has the most positive mean $\delta^{18}\text{O}$ value at $23.9\text{‰} \pm 2.6\text{‰}$ and a range from 21.1‰ to 27.5‰ for four samples. The taxon displaying the lowest mean $\delta^{18}\text{O}$ value is *Equus simplicidens*, which has a mean $\delta^{18}\text{O}$ value of $19.9\text{‰} \pm 4.3\text{‰}$ and a range from 17.7‰ to 22.1‰ for two samples. Similar to the $\delta^{13}\text{C}$ values, *Titanotylopus nebraskensis* and *Camelops* sp. have very similar $\delta^{18}\text{O}$ values (21.2‰ and 20.8‰ respectively).

Big Springs Locality

All sample means are significantly higher than *Platygonus* sp. ($-11.34\text{‰} \pm .74\text{‰}$) with a value range from -11.73‰ to -10.59‰ for three samples (Table 2I). Within the taxa present, *Stegomastodon* sp. has the most positive mean $\delta^{13}\text{C}$ value at $-1.7\text{‰} \pm 4.8\text{‰}$ and a range from -4.2‰ to $.8\text{‰}$ for two samples (Figure 11). Within the taxa present, *Platygonus* sp. has the most positive mean $\delta^{18}\text{O}$ value at $25.1\text{‰} \pm 2.2\text{‰}$ and a range from 23.4‰ to 27.2‰ for three samples. The taxon displaying the lowest mean $\delta^{18}\text{O}$ value is *E. simplicidens*, which has a mean $\delta^{18}\text{O}$ value of $22.0\text{‰} \pm .9\text{‰}$ and ranges from 20.5‰ to 23.4‰ for five samples.

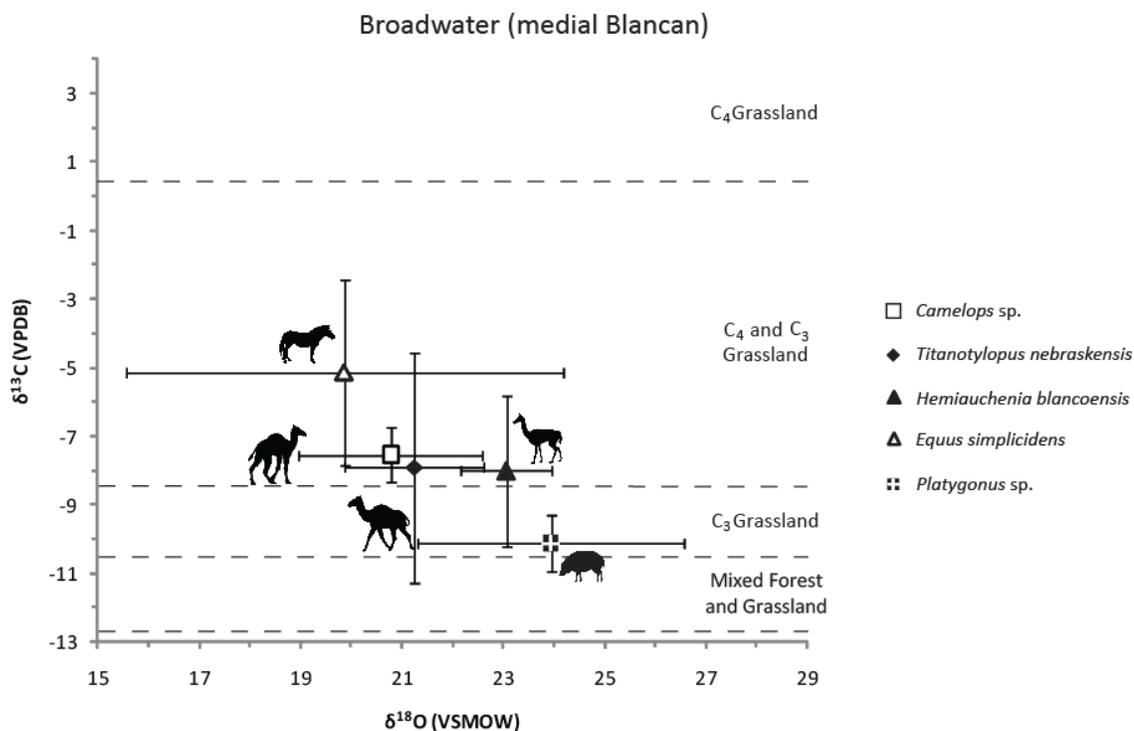


Figure 10: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from mammalian taxa at the Broadwater locality with interpreted habitats (Figure 4). Symbols represent the mean value; error bars represent 95% confidence (± 1.96 SE).

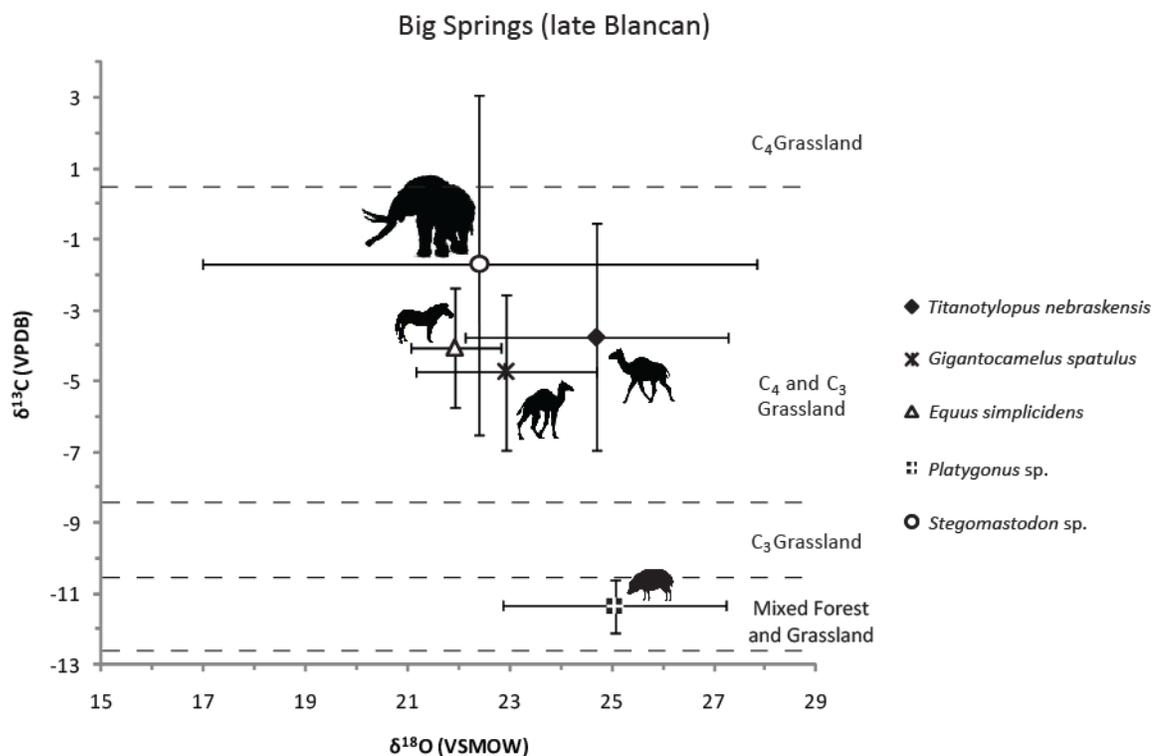


Figure 11: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from mammalian taxa at the Big Springs locality with interpreted habitats (Figure 4). Symbols represent the mean value; error bars represent 95% confidence (± 1.96 SE).

Serial Sampling

A total of 59 samples were taken from three *N. eurystyle* teeth from the Cambridge locality (Table 3, Appendix B). Three-point moving averages of the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values are shown in Figures 12 and 13 for these specimens, respectively. The first two samples from specimen UNSM 4016 gave very small CO_2 yields which could indicate that there was cementum or dentin in the sample, or that the enamel was decalcified in those spots. These two samples are not included in the analysis. Specimen UNSM 4016 has a mean $\delta^{13}\text{C}$ value of $-8.0\text{‰} \pm 0.1\text{‰}$ for 19 samples with a range from -8.4‰ to -7.3‰ . The mean $\delta^{18}\text{O}$ value is $27.2\text{‰} \pm 0.4\text{‰}$ with a range from 25.9‰ to 28.9‰ . Specimen UNSM 4015 has a mean $\delta^{13}\text{C}$ value of $-9.3\text{‰} \pm 0.1\text{‰}$ for 21 samples with a range from -9.6‰ to -8.9‰ . The mean $\delta^{18}\text{O}$ value is $24.8\text{‰} \pm 0.8\text{‰}$ with a range from 21.8‰ to 27.3‰ . Specimen UNSM 4017 has a mean $\delta^{13}\text{C}$ value of $-8.5\text{‰} \pm 0.3\text{‰}$ for 19 samples with a range from -9.0‰ to -7.0‰ . The mean $\delta^{18}\text{O}$ value is $24.1\text{‰} \pm 0.3\text{‰}$ with a range from 21.0‰ to 27.5‰ .

Table 3: Serial carbon and oxygen isotope variation, per individual.

Taxon	UNSM no.	<i>n</i>	$\delta^{13}\text{C}$ (‰)			$\delta^{18}\text{O}$ (‰)		
			Min.	Max.	Range	Min.	Max.	Range
<i>N. eurystyle</i>	4015	21	-9.61	-8.86	0.75	21.84	27.26	5.42
<i>N. eurystyle</i>	4016	19	-8.39	-7.33	1.06	25.92	28.93	3.01
<i>N. eurystyle</i>	4017	19	-9.05	-7.07	1.97	20.96	27.53	6.57
<i>E. simplicidens</i>	52140	25	-7.71	-5.60	2.11	18.97	22.33	3.36
<i>E. simplicidens</i>	46810	21	-2.73	1.12	1.61	21.47	25.51	4.04
<i>E. simplicidens</i>	2043-92	17	-3.55	-2.33	1.22	21.23	23.63	2.40

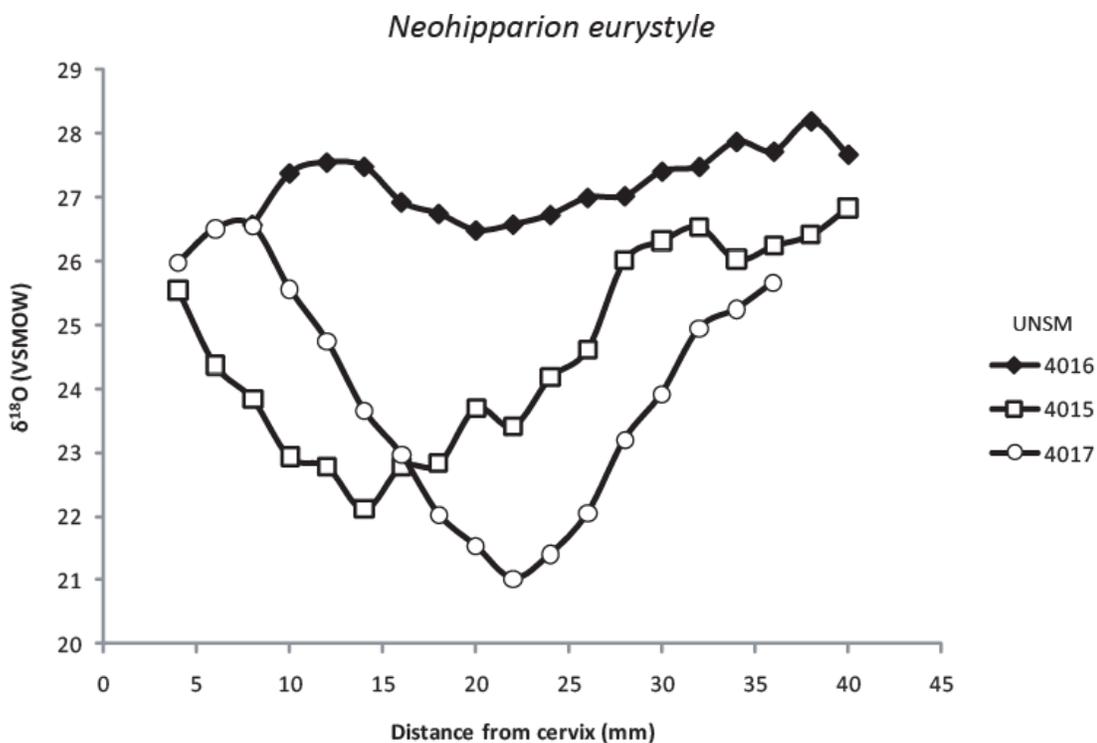


Figure 12: Serial samples of oxygen isotope ratios ($\delta^{18}\text{O}$) for *Neohipparion eurystyle* from the Cambridge locality.

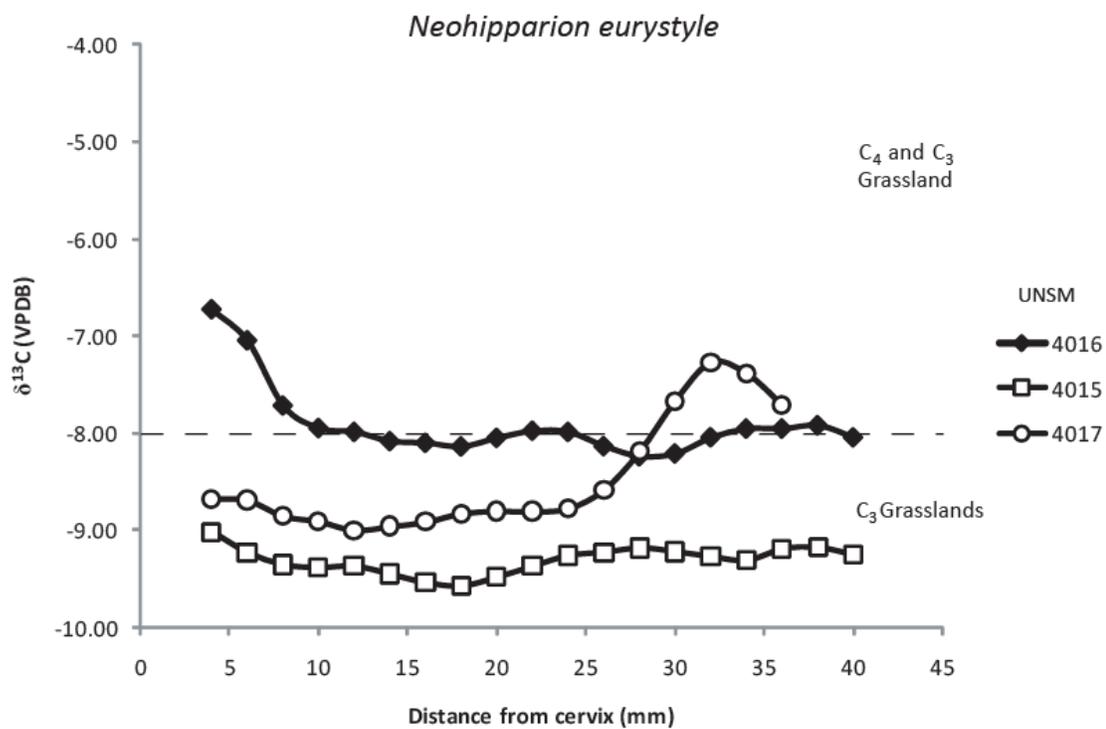


Figure 13: Serial samples of carbon isotope ratios ($\delta^{13}\text{C}$) for *Neohipparion eurystyle* from the Cambridge locality with interpreted habitats.

A total of 63 samples were taken from three *Equus simplicidens* teeth from the Big Springs locality. Three point moving averages of the $\delta^{18}\text{O}$ values are shown in Figures 14 and 15 for these specimens respectively. Specimen UNSM 52140 has a mean $\delta^{13}\text{C}$ value of $-6.4\text{‰} \pm 0.3\text{‰}$ for 25 samples with a range from -7.7‰ to -5.6‰ (Table 3, Appendix B). The mean $\delta^{18}\text{O}$ value is $20.5\text{‰} \pm 0.4\text{‰}$ with a range from 19.0‰ to 22.3‰ . Specimen UNSM 46810 has a mean $\delta^{13}\text{C}$ value of $-1.8\text{‰} \pm 0.2\text{‰}$ for 21 samples with a range from -2.7‰ to -1.2‰ . The mean $\delta^{18}\text{O}$ value is $23.4 \pm 0.5\text{‰}$ with a range from 21.5‰ to 25.5‰ . Specimen UNSM 2043-92 has a mean $\delta^{13}\text{C}$ value of $-3.0\text{‰} \pm 0.2\text{‰}$ for 17 samples with a range from -3.6‰ to -2.3‰ . The mean $\delta^{18}\text{O}$ value is $22.2\text{‰} \pm 0.3\text{‰}$ with a range from 21.2‰ to 23.6‰ .

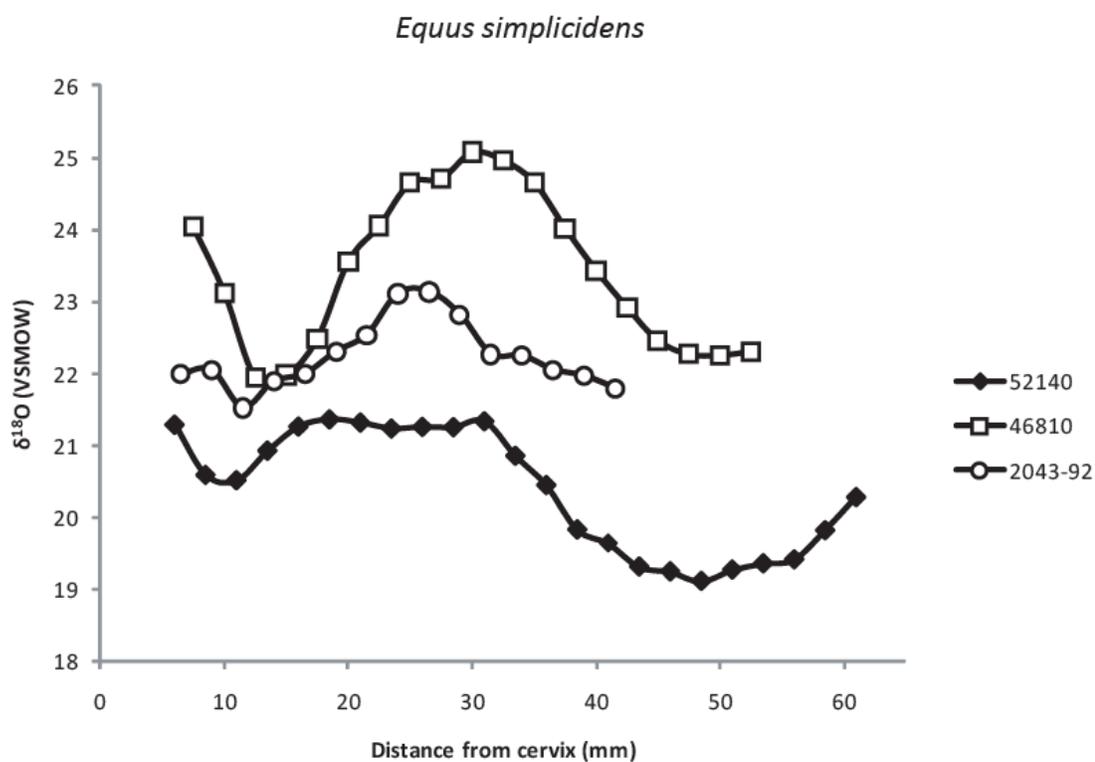


Figure 14: Serial samples of oxygen isotope ratios ($\delta^{18}\text{O}$) for *Equus simplicidens* from the Big Springs locality.

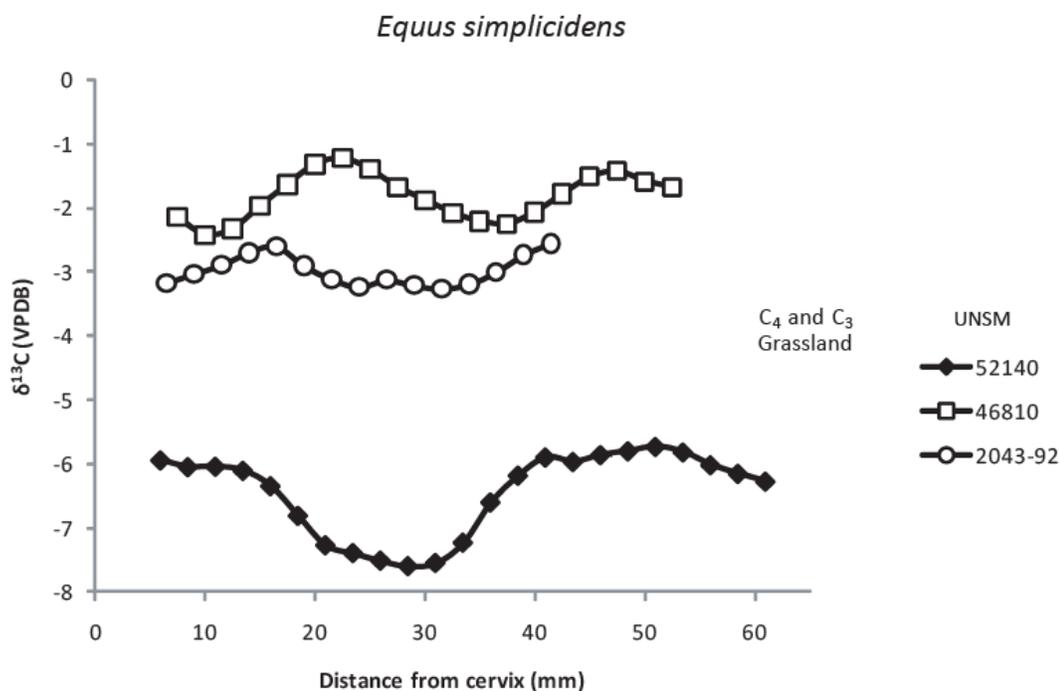


Figure 15: Serial samples of carbon isotope ratios ($\delta^{13}\text{C}$) for *Equus simplicidens* from the Big Springs locality with interpreted habitats.

DISCUSSION

Bulk Sampling

Mean $\delta^{13}\text{C}$ values from the late Miocene localities (North Shore, Pratt Slide, Cambridge) indicate that taxa were exclusively consuming C₃ vegetation (Figure 5), as expected from previous work in the area (Passey et al., 2002; Fox and Koch, 2004). Based on the low mean $\delta^{13}\text{C}$ value, Pratt Slide appears to be the most closed of all Miocene localities, between a mixed grassland and forest and open forest habitat. Pratt Slide is the most northern of all Miocene localities (Figure 1) indicating that while some of southern Nebraska had more open, grassland habitats, northern Nebraska could have

had a more wooded or forested habitat during the late Miocene. In contrast, mean $\delta^{13}\text{C}$ values from the Pliocene indicate that taxa generally consumed at least a partial diet of C_4 vegetation and grassland habitats were dominant.

There is a marked shift to lower mean $\delta^{18}\text{O}$ values from the Miocene to the Pliocene, a pattern previously reported in horse teeth between the Barstovian and Blancan land-mammal ages (Passey et al. 2002). This shift to lower $\delta^{18}\text{O}$ values is consistent with the expectations for global cooling from the Miocene to the Pleistocene; a similar interpretation was made using soil carbonates from the Great Plains (Fox and Koch, 2004).

North Shore Locality

The mean $\delta^{13}\text{C}$ values indicate that all taxa were consuming C_3 vegetation in the North Shore locality. The statistically significant differences observed among taxa suggest different diets, use of different habitats, or both. Distinguishing riparian from forested habitats isotopically can be difficult, but patterns observed in both modern and ancient environments suggest that relatively higher $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values likely indicate residence in more open habitats, whereas lower $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values indicate habitation of more closed environments (Cerling et al., 2004; Feranec and MacFadden, 2006; Feranec, 2007) . All of the taxa in this locality have mean $\delta^{13}\text{C}$ values that indicate a C_3 grassland to mixed grassland and forest habitat (Figure 6). Within the mixed zone, *Serbelodon* cf. *S. barbourensis* appears to be occupying the most closed environment of the taxa present, which agrees with predictions of it being a mixed feeder (Table 4). It

has the lowest mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, significantly lower than *Cormohipparion occidentale* (expected to be a mixed feeder; Table 4), which appears to be living in a grassland. *Serbelodon* cf. *S. barbourensis* could have possibly been living a semi-aquatic lifestyle based on the model to determine aquatic habitats using stable isotopes from Clementz et al. (2008) (Figure 16), in agreement with tusk wear patterns in Lambert (1992) suggesting that *Serbelodon* was a generalized feeder that sometimes consumed aquatic plants by scooping them with its shovel-tusks. Both *Megatylopus* cf. *M. primaevus* and *Aphelops* sp. are considered browsers (Table 4), which would be possible in the mixed grassland and forest habitat. *Teleoceras major* appears to be living in a C_3 grassland, agreeing with the presumption that it was a grazer.

Pratt Slide Locality

Pratt Slide has a lower mean $\delta^{13}\text{C}$ value than North Shore, which indicates that Pratt Slide falls on the boundary between a mixed forest and grassland and open forest habitat (Figure 7). This interpretation agrees with presumed browsing and mixed diets, of the taxa present, from previous studies (Table 4). The data also show that *Cormohipparion*, present in both Clarendonian localities, had the ability to live in different environments. This equid has the highest $\delta^{13}\text{C}$ values in North Shore, but the lowest in Pratt Slide indicating that it can live in either open grassland or in an open forest habitat. The other equid in Pratt Slide, *Hipparion* sp., appears to have lived

Table 4: Dietary interpretations for taxa in this study based on previous work.

Taxa	Presumed Diet	Method determined	Reference
Equidae			
<i>Calippus</i>	Grazer	Stable Isotopes	Feranec and MacFadden 2006
<i>Cormohipparion</i>	Mixed Feeder	Stable Isotopes	MacFadden and Cerling 1996
<i>Equus</i>	Grazer	Stable Isotopes	MacFadden and Cerling 1996, Passey et al. 2002
<i>Hipparion</i>	Mixed Feeder	Stable Isotopes	MacFadden and Cerling 1996
<i>Neohipparion</i>	Grazer	Hypsodonty & Microwear	MacFadden et al. 1999
Rhinocerotidae			
<i>Aphelops</i>	Browser	Hypsodonty & Stable Isotopes	MacFadden 1998
<i>Teleoceras</i>	Mixed Feeder / Grazer	Hypsodonty & Stable Isotopes	MacFadden 1998
Gomphotheriidae			
<i>Serbelodon</i>	Mixed Feeder	Wear Patterns on Shovel Tusks	Lambert 1992
<i>Stegomastodon</i>	Mixed Feeder	Stable Isotopes	Prado et al. 2005
Camelidae			
<i>Alforjas</i>	Browser	Premaxillary Shape	Dompierre and Churcher 1996
<i>Camelops</i>	Browser	Hypsodonty, Microwear & Mesowear	Semprebon and Rivals 2010
<i>Gigantocamelus</i>	Browser or Grazer	Microwear & Mesowear Hypsodonty	Semprebon and Rivals 2010 Voorhies and Corner 1986
<i>Megatylopus</i>	Browser	Hypsodonty, Microwear & Mesowear	Semprebon and Rivals 2010
<i>Hemiauchenia</i>	Mixed Feeder / Browser	Hypsodonty, Microwear, Mesowear & Stable Isotopes	Feranec 2003, Semprebon and Rivals 2010
<i>Procamelus</i>	Browser	Hypsodonty, Microwear & Mesowear	Semprebon and Rivals 2010
<i>Titanotylopus</i>	Browser	Hypsodonty	Barbour and Schultz 1934
Palaeomerycidae			
<i>Cranioceras</i>	Browser / Mixed Feeder	Microwear & Mesowear	Semprebon et al. 2004
Tayassuidae			
<i>Platygonus</i>	Mixed Feeder	Hypsodonty & Stable Isotopes	MacFadden and Cerling 1996
<i>Prosthennops</i>	Browser	Stable Isotopes	MacFadden and Cerling 1996

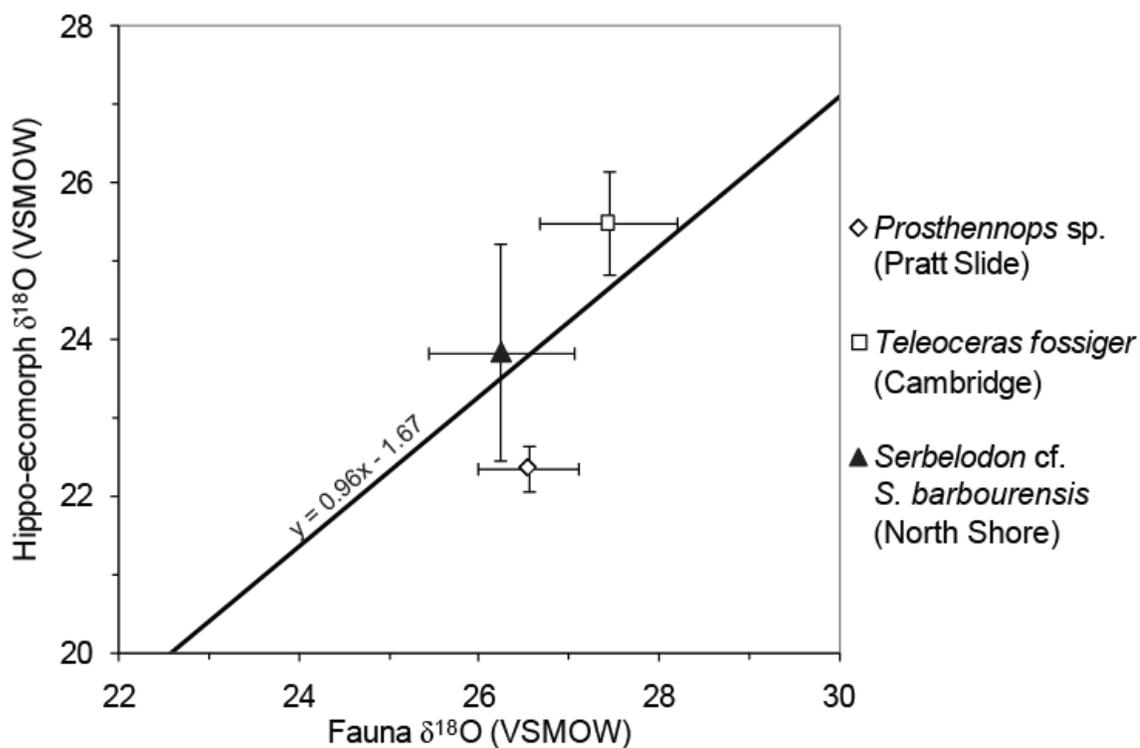


Figure 16: Bivariate plot of mean $\delta^{18}\text{O}$ values for three hippo ecomorphs and associated faunas. Solid black line represents the relationships between mean faunal $\delta^{18}\text{O}$ values vs. hippopotamid $\delta^{18}\text{O}$ values presented in Figure 4 from Clementz et al. (2008). Modified from Clementz et al. (2008).

on the boundary between a mixed forest and grassland and an open forest habitat, agreeing with previous interpretations that it was a mixed feeder (Table 4). *Teleoceras major*, seen in both late Clarendonian localities, has a mean $\delta^{13}\text{C}$ value that is 2‰ lower in Pratt Slide than in North Shore, supporting the idea that Pratt Slide was a more closed environment than North Shore.

Prosthennops sp. has a significantly lower mean $\delta^{18}\text{O}$ value than all other taxa in Pratt Slide (Table 2D). This could be indicative of feeding in a semi-aquatic habitat using the model of Clementz et al. (2008) (Figure 16). This is in stark contrast to

Prosthennops sp. from the late Miocene in California (Feranec and MacFadden, 2006) and the middle Miocene of Florida (Clementz et al., 2008) where the $\delta^{18}\text{O}$ values are not statistically different from any other taxa. These results imply that *Prosthennops* sp. was living a much different lifestyle in the Great Plains of Nebraska than in other regions of North America during the Miocene or that these were very different species of *Prosthennops* that have not been identified to species level.

Cambridge Locality

The mean $\delta^{13}\text{C}$ value for the Cambridge Locality is similar to North Shore and about 2‰ higher than Pratt Slide suggesting that Cambridge falls mainly in the grassland habitat with some taxa in the mixed forest and grassland habitat (Figure 8). The two equids, *Neohipparion eurystyle* and *Calippus* sp., have the highest mean $\delta^{13}\text{C}$ values among the taxa present. This would suggest that the two equids could be grazing, which agrees with previous dietary interpretations (Table 4). In contrast to the grazing lifestyle that would be needed to survive in a very open grassland habitat, *Aphelops mutilus*, *Alforjas* sp., and *Megatylopus* sp. are all presumed browsers (Table 4). Cambridge appears to have some browse, which could possibly support these taxa. *Teleoceras fossiger* was a presumed grazer or mixed feeder (Table 4), agreeing with the grassland to mixed habitat predicted here. *Hemiauchenia* cf. *H. vera* has the lowest mean $\delta^{13}\text{C}$ value and is significantly different from both of the equids, while falling just below the boundary for a mixed grassland to forest habitat, agreeing with previous dietary interpretations that it was a mixed feeder or browser (Table 4). Among the taxa in

Cambridge, *N. eurystyle* has the lowest mean $\delta^{18}\text{O}$ value and is similar to presumed water dependent taxa (*A. mutilus* and *T. fossiger*) suggesting that this horse got most of its water from drinking. In contrast, *Calippus* sp. has the highest mean $\delta^{18}\text{O}$ value, similar to presumed evaporation sensitive taxa (*Alforjas* sp. and *Megatylopus* sp.), suggesting that it was getting a large portion of its water from plants. *Teleoceras fossiger* has been presumed to be semi-aquatic because it had a very similar body type to modern hippos, but in agreement with Clementz et al. (2008), the model shows that it was probably not semi-aquatic (Figure 16).

Lisco Locality

Gigantocamelus spatulus is the only taxon sampled in Lisco and had a mixed diet of C_4 and C_3 vegetation (Figure 9). While only one taxon was sampled, these $\delta^{13}\text{C}$ values indicate that C_4 grasslands spread in Nebraska between the middle Hemphillian and the beginning of the Blancan. A mean $\delta^{13}\text{C}$ value of -3.1 agrees with the expectation by Voorhies and Corner (1986) that *G. spatulus* was a grazer while in contrast with Semprebon and Rivals (2010) assumption that it was a browser (Table 4).

Broadwater Locality

The taxa in the Broadwater locality yield mean $\delta^{13}\text{C}$ values that suggest habitats ranging from pure C_3 grasslands to mixed C_3/C_4 grasslands (Figure 10). This range is interesting because even though Broadwater is very close geographically to Lisco (Figure

1), the taxa were consuming a smaller portion of C₄ vegetation than *Gigantocamelus spatulus*. The only equid, *Equus simplicidens*, has a mean $\delta^{13}\text{C}$ value within the C₃/C₄ grassland range. The results are compatible with previous work that it was a presumed grazer (Table 4). *Titanotylopus nebraskensis* and *Camelops* sp. have mean $\delta^{13}\text{C}$ values that fall in the C₃/C₄ grassland habitat disagreeing with previous work suggesting that each of these taxa were browsers (Table 4). *Platygonus* sp. has the lowest mean $\delta^{13}\text{C}$ value, consistent with a pure C₃ diet, and falls into the lower range of the C₃ habitat. This agrees with its presumed diet of being a mixed feeder (Table 4). Of the taxa present, *Platygonus* sp. has the highest mean $\delta^{18}\text{O}$ value in Broadwater. This is unexpected since it appears to be consuming C₃ vegetation and C₄ plants generally result in higher $\delta^{18}\text{O}$ values (Helliker and Ehleringer, 2002). So, it could be consuming fruits or other more evaporated C₃ plants. Another explanation could be that *Platygonus* sp. is the most evaporation-sensitive taxa. This seems unlikely because *Platygonus* sp. appears to have been living in a riparian environment. Further research on this peccary and the paleoenvironments of the Broadwater locality will likely illuminate this problem.

Big Springs

Several of the taxa from Big Springs yield mean $\delta^{13}\text{C}$ values suggesting a C₃/C₄ grassland habitat (Figure 11). These mean $\delta^{13}\text{C}$ values are unexpected based on work by Teeri and Stowe (1976), indicating that less than 40% of all grass species at latitudes similar to northern Nebraska would be C₄ grasses. Among the taxa present, *Stegomastodon* sp. has the highest mean $\delta^{13}\text{C}$ value in the C₃/C₄ grassland habitat, but

due to small sample size it has a very large 95% confidence interval that extends into the pure C₄ grassland habitat. This prediction of grassland habitat for *Stegomastodon* sp., corresponds with presumptions that it could both browse and graze (Table 4). *Stegomastodon* sp. appears to have lived in a very different environment than the earlier proboscidean, *Serbelodon* cf. *S. barbourensis*.

The equid, *Equus simplicidens*, and the two camelids, *Titanotylopus nebraskensis* and *Gigantocamelus spatulus*, all have mean $\delta^{13}\text{C}$ values that fall into the C₃/C₄ grassland habitat (Figure 11). *Equus simplicidens* of Big Springs has a very similar mean $\delta^{13}\text{C}$ value to *E. simplicidens* in Broadwater. This indicates that while Broadwater appears to have a lower percentage of C₄ biomass, this equid had a very similar diet in both localities. The camelids in Big Springs both have higher mean $\delta^{13}\text{C}$ values than the camelids in Broadwater, and both taxa fall within the grasslands habitat (Figure 11), which is in stark contrast to previous work suggesting that *T. nebraskensis* was probably a browser (Table 4). *Gigantocamelus spatulus* was presumed to be a grazer by Voorhies and Corner (1986) (Figure 11), agreeing with a mean $\delta^{13}\text{C}$ value of -4.7‰. *Titanotylopus nebraskensis* has a mean $\delta^{13}\text{C}$ value 4‰ higher in Big Springs compared to Broadwater. This would indicate that *T. nebraskensis* is able to browse or a graze depending on the habitat space. In Big Springs, *G. spatulus* has a mean $\delta^{13}\text{C}$ value approximately 1.5‰ lower than in Lisco suggesting that this camelid probably grazed at both localities.

In Big Springs, *Platygonus* sp. has a significantly lower mean $\delta^{13}\text{C}$ value from all other taxa, consistent with a pure C₃ diet. It falls on the border between C₃ grassland and open woodland habitat (Figure 11) indicating that *Platygonus* at this locality was a browser to mixed feeder with agrees with previous work (Table 4). The mean $\delta^{13}\text{C}$ value

is similar to the Broadwater specimens of *Platygonus* sp., but is approximately 1‰ lower. This indicates that while several taxa have taken advantage of the expansion of C₄ grasslands, there must still be wooded habitats in this area. Given the predominance of grazing taxa at the Big Springs locality, suggesting a mostly open habitat, it is likely that there were only small patches of forest present, probably along rivers or springs.

Serial Sampling

The serial samples of *Neohipparion eurystyle* teeth reflect seasonal differences in monthly temperatures and / or precipitation with $\delta^{18}\text{O}$ values that range from 3.0‰ to 6.5‰ (Table 3). The peaks are interpreted as the summer months and the troughs are interpreted as the winter months, with spring and fall months between. These *N. eurystyle* specimens appear to be recording approximately 1 year of growth and mineralization, which is slightly less than modern horses (Hillson, 2005). Only having one year of data indicates that approximately one year of growth is ground off of these teeth because of wear, or that the teeth of this equid only record one year of growth.

The $\delta^{13}\text{C}$ values can be used to determine whether seasonal variation is present in the diet of *Neohipparion eurystyle*. All of the $\delta^{13}\text{C}$ values for the three specimens fall in the grassland habitat range (Figure 13). There is some variation in $\delta^{13}\text{C}$ (between 0.8‰ and 2.0‰, Table 3) suggesting that these taxa were probably not changing their diet or migrating throughout the year to eat different diets, similar to the equids studied in Feranec et al. (2009). The variations observed, particularly in specimen UNSM 4017,

appear to follow the seasonal variation pattern seen in Figure 12 indicating that it was due to plants becoming more water-stressed in the warmer summer months.

The serial samples of *Equus simplicidens* teeth also show seasonal variation in the $\delta^{18}\text{O}$ values, although the variation (2.40‰ to 4.04‰) is not as drastic as for *Neohipparion eurystyle*. The data show that third molars take about a year and a half to mineralize in *E. simplicidens*, which is the same as in modern horses (Hillson, 2005). While the number of samples is fairly small, the data imply that seasonal variation was not as great in the late Pliocene as in the late Miocene. However, a larger sample size in both *N. eurystyle* and *E. simplicidens* is needed to better understand seasonal variation in these areas.

The $\delta^{13}\text{C}$ values show small variations (1.2‰ to 2.1‰) in diet for *Equus simplicidens*. In contrast to *Neohipparion eurystyle*, the $\delta^{13}\text{C}$ values in *E. simplicidens* seem to have a reverse trend in comparison to the $\delta^{18}\text{O}$ values (Figures 14 and 15). Peaks in $\delta^{13}\text{C}$ match up with troughs in $\delta^{18}\text{O}$ values. While all specimens stay within the boundaries for a C_3/C_4 diet, UNSM 52140 appears to be consuming more C_3 vegetation than the other two specimens (Figure 14), suggesting that this individual consumed more C_4 vegetation in the presumed winter season.

CONCLUSIONS

Late Miocene taxa exclusively exploited C_3 vegetation and had habitat ranges from mixed grasslands and open forests (Pratt Slide) to C_3 grasslands (North Shore and Cambridge). Within the faunas of the C_3 -dominated localities, resource partitioning is

discernible on the basis of stable isotope values. Equids appear to have had a preference for open habitats and C₃ grazing in both North Shore and Cambridge. The equid *Cormohipparion* appears to have been able to exploit both grassland and open forest habitats. Camelids and rhinocerotids exploited niches ranging from mixed browsing and grazing to pure grazing. The gomphothere *Serbelodon* cf. *S. barbourensis* might have been semi-aquatic and fed in more closed environments than other taxa at North Shore. Rhinocerotids have consistently lower mean $\delta^{18}\text{O}$ values in the late Miocene suggesting water dependence, while camelids have higher mean $\delta^{18}\text{O}$ values suggesting that they relied more on food for their water. The peccary *Prosthennops* sp., in Pratt Slide, has a very low mean $\delta^{18}\text{O}$ value with extremely low variance, suggesting a semi-aquatic existence.

The spread of C₄ grasslands in the Blancan is recorded by many taxa that switched their diet from C₃ grasses or evolved adaptations for grazing. Several camelids, the equid *Equus simplicidens*, and the gomphothere *Stegomastodon* sp., were consuming C₄ vegetation in the Blancan. Although C₄ vegetation was consumed by many taxa, C₃ vegetation remained sufficient in the Blancan to support the C₃ mixed feeder, *Platygonus* sp. This pattern could be indicative of riparian habitats surrounded by C₄ grasslands.

There is a marked shift to lower mean $\delta^{18}\text{O}$ values from the Miocene to the Pliocene, a pattern consistent with the expectations for global cooling from the Miocene to the Pleistocene. In addition, $\delta^{18}\text{O}$ values from serial samples suggest that seasonality decreased from the Miocene to the Pliocene. These data agree with previous studies indicating global change in climate and vegetation from the late Miocene to the Pliocene.

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APPENDIX A

BULK SAMPLING $\delta^{13}\text{C}$ AND $\delta^{18}\text{O}$ VALUES

Table 5: Museum number, taxon, locality, and stable carbon and oxygen isotope compositions for each sample analyzed in this study

UNSM no.	Taxon	Locality	$\delta^{13}\text{C}$ (VPDB)	$\delta^{18}\text{O}$ (VPDB)	$\delta^{18}\text{O}$ (VSMOW)
97051	<i>Aphelops</i> sp.	North Shore	-10.88	-4.50	26.27
8286-92	<i>Aphelops</i> sp.	North Shore	-9.03	-4.61	26.16
97050	<i>Aphelops</i> sp.	North Shore	-9.40	-8.07	22.59
97040	<i>Cormohipparion occidentale</i>	North Shore	-9.26	-2.07	28.78
94382	<i>Cormohipparion occidentale</i>	North Shore	-9.22	-4.26	26.52
94394	<i>Cormohipparion occidentale</i>	North Shore	-8.37	-4.90	25.86
97044	<i>Cormohipparion occidentale</i>	North Shore	-9.31	-3.26	27.55
94365	<i>Cormohipparion occidentale</i>	North Shore	-8.60	-6.09	24.63
9539-89	<i>Megatylopus</i> cf. <i>M. primaevus</i>	North Shore	-9.66	-4.87	25.89
9506-89	<i>Megatylopus</i> cf. <i>M. primaevus</i>	North Shore	-9.07	-4.34	26.44
94235	<i>Megatylopus</i> cf. <i>M. primaevus</i>	North Shore	-10.29	-1.14	29.73
1001-002	<i>Serbelodon</i> cf. <i>S. barbourensis</i>	North Shore	-10.80	-7.54	23.14
1193-000	<i>Serbelodon</i> cf. <i>S. barbourensis</i>	North Shore	-10.16	-6.18	24.54
8962-92	<i>Teleoceras major</i>	North Shore	-8.97	-6.33	24.39
97071	<i>Teleoceras major</i>	North Shore	-8.38	-4.82	25.95
94295	<i>Teleoceras major</i>	North Shore	-9.85	-4.51	26.27
8176-92	<i>Teleoceras major</i>	North Shore	-9.36	-5.94	24.78
97072	<i>Teleoceras major</i>	North Shore	-8.98	-4.77	25.99
117939	<i>Cormohipparion</i> sp.	Pratt Slide	-12.26	-4.81	25.95
117940	<i>Cormohipparion</i> sp.	Pratt Slide	-12.96	-5.48	25.26
133000	<i>Cranioceras unicornis</i>	Pratt Slide	-13.15	-4.42	26.35
133001	<i>Cranioceras unicornis</i>	Pratt Slide	-14.50	-3.04	27.77
133007	<i>Cranioceras unicornis</i>	Pratt Slide	-11.36	-4.52	26.25
133008	<i>Cranioceras unicornis</i>	Pratt Slide	-11.65	-3.60	27.20
133009	<i>Cranioceras unicornis</i>	Pratt Slide	-11.44	-3.09	27.72
5018-89A	<i>Hipparion</i> sp.	Pratt Slide	-11.29	-4.34	26.43
5024-89B	<i>Hipparion</i> sp.	Pratt Slide	-12.55	-5.45	25.29
5024-89C	<i>Hipparion</i> sp.	Pratt Slide	-11.05	-4.15	26.63
5024-89A	<i>Procamelus grandis</i>	Pratt Slide	-10.15	-3.56	27.24
5018-89B	<i>Procamelus grandis</i>	Pratt Slide	-11.65	-3.80	26.99
5030-89	<i>Procamelus grandis</i>	Pratt Slide	-10.87	-2.25	28.59
5024-89C	<i>Procamelus grandis</i>	Pratt Slide	-12.20	-3.78	27.02
133003	<i>Prosthenlops</i> sp.	Pratt Slide	-11.61	-8.25	22.41
133002	<i>Prosthenlops</i> sp.	Pratt Slide	-11.46	-7.95	22.72
133006	<i>Prosthenlops</i> sp.	Pratt Slide	-11.68	-8.65	21.99
133004	<i>Prosthenlops</i> sp.	Pratt Slide	-11.28	-8.34	22.31
5018-89B	<i>Teleoceras major</i>	Pratt Slide	-11.07	-4.34	26.44
2112-94	<i>Teleoceras major</i>	Pratt Slide	-11.57	-7.20	23.49

Table 5: Continued

UNSM no.	Taxon	Locality	$\delta^{13}\text{C}$ (VPDB)	$\delta^{18}\text{O}$ (VPDB)	$\delta^{18}\text{O}$ (VSMOW)
1252-47A	<i>Alforjas</i> sp.	Cambridge	-9.86	-1.90	28.95
1252-47B	<i>Alforjas</i> sp.	Cambridge	-10.32	-3.11	27.71
5812	<i>Aphelops mutilus</i>	Cambridge	-10.54	-4.68	26.08
1187-47	<i>Aphelops mutilus</i>	Cambridge	-10.13	-4.37	26.40
4162	<i>Calippus</i> sp.	Cambridge	-9.73	-0.91	29.97
4179	<i>Calippus</i> sp.	Cambridge	-9.56	-2.77	28.05
672-48	<i>Hemiauchenia</i> cf. <i>H. vera</i>	Cambridge	-10.35	-1.81	29.05
1405-47	<i>Hemiauchenia</i> cf. <i>H. vera</i>	Cambridge	-11.19	-4.53	26.24
807-47	<i>Hemiauchenia</i> cf. <i>H. vera</i>	Cambridge	-11.83	-4.13	26.65
635-48	<i>Megatylopus</i> sp.	Cambridge	-10.48	-3.17	27.64
707-48	<i>Megatylopus</i> sp.	Cambridge	-9.63	-2.08	28.76
1250-47	<i>Megatylopus</i> sp.	Cambridge	-10.50	-3.05	27.77
2988	<i>Neohipparion eurystyle</i>	Cambridge	-8.80	-4.73	26.03
4071	<i>Neohipparion eurystyle</i>	Cambridge	-9.14	-6.01	24.72
4016	<i>Neohipparion eurystyle</i>	Cambridge	-8.01	-3.63	27.17
4015	<i>Neohipparion eurystyle</i>	Cambridge	-9.29	-5.93	24.79
4017	<i>Neohipparion eurystyle</i>	Cambridge	-8.46	-6.62	24.08
5819	<i>Teleoceras fossiger</i>	Cambridge	-8.66	-5.14	25.61
5821	<i>Teleoceras fossiger</i>	Cambridge	-9.98	-5.87	24.86
5820B	<i>Teleoceras fossiger</i>	Cambridge	-10.85	-4.41	26.36
5820A	<i>Teleoceras fossiger</i>	Cambridge	-10.50	-5.61	25.13
18409-39	<i>Gigantocamelus spatulus</i>	Lisco	-2.92	-7.59	23.08
9913-38	<i>Gigantocamelus spatulus</i>	Lisco	-2.06	-7.47	23.21
11690-38	<i>Gigantocamelus spatulus</i>	Lisco	-3.97	-8.26	22.39
133010	<i>Gigantocamelus spatulus</i>	Lisco	-2.10	-7.21	23.48
379-41	<i>Gigantocamelus spatulus</i>	Lisco	-4.46	-8.23	22.42
1072-40	<i>Camelops</i> sp.	Broadwater	-7.95	-8.93	21.71
4935-38	<i>Camelops</i> sp.	Broadwater	-7.13	-10.72	19.86
122056	<i>Equus simplicidens</i>	Broadwater	-3.77	-8.59	22.05
2528-41	<i>Equus simplicidens</i>	Broadwater	-6.51	-12.86	17.65
125882	<i>Hemiauchenia blancoensis</i>	Broadwater	-10.04	-7.19	23.50
125709	<i>Hemiauchenia blancoensis</i>	Broadwater	-10.61	-9.21	21.41
125847	<i>Hemiauchenia blancoensis</i>	Broadwater	-4.79	-6.31	24.40
125830	<i>Hemiauchenia blancoensis</i>	Broadwater	-10.65	-7.45	23.23
125742	<i>Hemiauchenia blancoensis</i>	Broadwater	-5.32	-6.89	23.81
125846	<i>Hemiauchenia blancoensis</i>	Broadwater	-6.69	-8.66	21.98
53653	<i>Platygonus</i> sp.	Broadwater	-9.72	-7.62	23.05
53651	<i>Platygonus</i> sp.	Broadwater	-10.02	-3.31	27.49
53645	<i>Platygonus</i> sp.	Broadwater	-9.45	-9.56	21.05
7793-39	<i>Platygonus</i> sp.	Broadwater	-11.30	-6.56	24.14
89123	<i>Titanotylopus nebraskensis</i>	Broadwater	-6.19	-8.70	21.94
89118	<i>Titanotylopus nebraskensis</i>	Broadwater	-9.64	-10.06	20.54

Table 5: Continued

UNSM no.	Taxon	Locality	$\delta^{13}\text{C}$ (VPDB)	$\delta^{18}\text{O}$ (VPDB)	$\delta^{18}\text{O}$ (VSMOW)
46848	<i>Equus simplicidens</i>	Big Springs	-6.78	-9.78	20.83
4143-86	<i>Equus simplicidens</i>	Big Springs	-4.16	-8.12	22.54
46849	<i>Equus simplicidens</i>	Big Springs	-2.24	-8.55	22.10
52410	<i>Equus simplicidens</i>	Big Springs	-6.43	-10.12	20.47
46810	<i>Equus simplicidens</i>	Big Springs	-1.81	-7.27	23.42
2043-92	<i>Equus simplicidens</i>	Big Springs	-2.97	-8.43	22.22
27539	<i>Gigantocamelus spatulus</i>	Big Springs	-5.01	-7.79	22.88
27536	<i>Gigantocamelus spatulus</i>	Big Springs	-3.00	-6.33	24.38
27533	<i>Gigantocamelus spatulus</i>	Big Springs	-8.83	-7.30	23.39
27553	<i>Gigantocamelus spatulus</i>	Big Springs	-4.39	-11.04	19.53
27542	<i>Gigantocamelus spatulus</i>	Big Springs	-2.47	-6.29	24.43
51643	<i>Platygonus</i> sp.	Big Springs	-11.70	-7.31	23.38
54937	<i>Platygonus</i> sp.	Big Springs	-11.73	-3.62	27.18
3021-98	<i>Platygonus</i> sp.	Big Springs	-10.59	-6.12	24.61
27556	<i>Stegomastodon</i> sp.	Big Springs	0.75	-5.56	25.18
3061-98	<i>Stegomastodon</i> sp.	Big Springs	-4.15	-10.95	19.62
46878	<i>Titanotylopus nebraskensis</i>	Big Springs	-2.41	-4.75	26.01
46879	<i>Titanotylopus nebraskensis</i>	Big Springs	-0.11	-4.43	26.35
46880	<i>Titanotylopus nebraskensis</i>	Big Springs	-5.97	-10.80	19.77
27650	<i>Titanotylopus nebraskensis</i>	Big Springs	-8.98	-6.45	24.26
2213-94	<i>Titanotylopus nebraskensis</i>	Big Springs	-1.32	-3.69	27.10

APPENDIX B

SERIAL SAMPLING $\delta^{13}\text{C}$ AND $\delta^{18}\text{O}$ VALUES

Table 6: Museum number, taxon, locality, distance from cervix, and stable carbon and oxygen isotope compositions for each sample analyzed in this study. * indicates that samples gave very small CO₂ yields and were excluded from the study.

UNSM no.	Taxon	Locality	Distance from cervix (mm)	$\delta^{13}\text{C}$ (VPDB)	$\delta^{18}\text{O}$ (VPDB)	$\delta^{18}\text{O}$ (VSMOW)
4016	<i>Neohipparion eurystyle</i>	Cambridge	2	*-6.95	*-6.40	*24.32
			4	*-5.92	*-0.84	*30.04
			6	-7.33	-4.84	25.92
			8	-7.90	-4.46	26.31
			10	-7.93	-3.35	27.46
			12	-8.02	-2.48	28.35
			14	-8.02	-3.97	26.82
			16	-8.22	-3.54	27.26
			18	-8.07	-4.11	26.68
			20	-8.13	-4.50	26.27
			22	-7.95	-4.30	26.48
			24	-7.85	-3.84	26.95
			26	-8.17	-4.06	26.72
			28	-8.39	-3.52	27.29
			30	-8.16	-3.76	27.03
			32	-8.08	-2.94	27.88
			34	-7.89	-3.30	27.51
			36	-7.90	-2.61	28.22
			38	-8.08	-3.39	27.42
			40	-7.79	-1.92	28.93
42	-8.27	-4.14	26.65			
4015	<i>Neohipparion eurystyle</i>	Cambridge	2	-8.86	-4.22	26.56
			4	-8.94	-5.31	25.43
			6	-9.27	-6.08	24.65
			8	-9.50	-7.64	23.03
			10	-9.30	-6.85	23.85
			12	-9.35	-8.73	21.91
			14	-9.46	-8.08	22.59
			16	-9.54	-8.80	21.84
			18	-9.61	-6.77	23.93
			20	-9.55	-7.96	22.71
			22	-9.28	-6.26	24.46
			24	-9.28	-7.59	23.08
			26	-9.23	-5.74	24.99
			28	-9.18	-4.97	25.79
			30	-9.15	-3.54	27.26
			32	-9.34	-4.84	25.92
			34	-9.33	-4.35	26.43
			36	-9.26	-5.03	25.73
			38	-8.99	-4.22	26.56
			40	-9.29	-3.86	26.93
42	-9.48	-3.79	27.00			

Table 6: Continued

UNSM no.	Taxon	Locality	Distance from cervix (mm)	$\delta^{13}\text{C}$ (VPDB)	$\delta^{18}\text{O}$ (VPDB)	$\delta^{18}\text{O}$ (VSMOW)
4017	<i>Neohipparion eurystyle</i>	Cambridge	2	-8.73	-5.95	24.78
			4	-8.53	-5.15	25.60
			6	-8.76	-3.28	27.53
			8	-8.78	-4.40	26.38
			10	-9.02	-5.03	25.73
			12	-8.92	-6.17	24.55
			14	-9.05	-6.75	23.95
			16	-8.90	-8.20	22.46
			18	-8.79	-8.18	22.48
			20	-8.78	-9.48	21.14
			22	-8.83	-9.64	20.97
			24	-8.81	-9.65	20.96
			26	-8.69	-8.37	22.28
			28	-8.25	-7.79	22.88
			30	-7.63	-6.28	24.43
			32	-7.12	-6.28	24.44
			34	-7.07	-4.83	25.93
36	-7.98	-5.38	25.36			
38	-8.09	-5.06	25.69			
52140	<i>Equus simplicidens</i>	Big Springs	3.5	-6.11	-8.32	22.33
			6	-5.85	-9.17	21.45
			8.5	-5.87	-10.49	20.10
			11	-6.43	-10.36	20.23
			13.5	-5.83	-9.39	21.23
			16	-6.06	-9.29	21.34
			18.5	-7.16	-9.38	21.24
			21	-7.23	-9.09	21.54
			23.5	-7.45	-9.42	21.20
			26	-7.53	-9.62	20.99
			28.5	-7.59	-9.02	21.61
			31	-7.71	-9.43	21.19
			33.5	-7.38	-9.38	21.24
			36	-6.63	-10.43	20.16
			38.5	-5.81	-10.62	19.96
			41	-6.11	-11.19	19.37
			43.5	-5.77	-10.98	19.59
			46	-6.03	-11.58	18.97
			48.5	-5.79	-11.38	19.17
51	-5.60	-11.37	19.19			
53.5	-5.82	-11.12	19.45			
56	-6.05	-11.13	19.44			
58.5	-6.20	-11.21	19.35			
61	-6.23	-9.94	20.66			
63.5	-6.41	-9.77	20.83			

Table 6: Continued

UNSM no.	Taxon	Locality	Distance from cervix (mm)	$\delta^{13}\text{C}$ (VPDB)	$\delta^{18}\text{O}$ (VPDB)	$\delta^{18}\text{O}$ (VSMOW)
46810	<i>Equus simplicidens</i>	Big Springs	5	-1.38	-6.43	24.28
			7.5	-2.34	-5.70	25.03
			10	-2.73	-7.88	22.79
			12.5	-2.20	-9.08	21.55
			15	-2.07	-9.15	21.47
			17.5	-1.65	-7.77	22.90
			20	-1.20	-7.60	23.08
			22.5	-1.12	-6.03	24.69
			25	-1.36	-6.31	24.40
			27.5	-1.72	-5.87	24.86
			30	-1.96	-5.87	24.85
			32.5	-1.95	-5.24	25.51
			35	-2.33	-6.19	24.53
			37.5	-2.36	-6.76	23.94
			40	-2.07	-7.09	23.60
			42.5	-1.78	-7.90	22.76
			45	-1.51	-8.26	22.39
			47.5	-1.28	-8.43	22.22
			50	-1.51	-8.45	22.20
52.5	-1.98	-8.31	22.34			
55	-1.54	-8.27	22.39			
2043-92	<i>Equus simplicidens</i>	Big Springs	4	-3.32	-9.21	21.41
			6.5	-3.04	-7.37	23.31
			9	-3.16	-9.39	21.23
			11.5	-2.90	-9.04	21.59
			14	-2.64	-8.89	21.74
			16.5	-2.56	-8.34	22.31
			19	-2.61	-8.73	21.91
			21.5	-3.55	-7.99	22.67
			24	-3.18	-7.66	23.02
			26.5	-2.98	-7.06	23.63
			29	-3.22	-7.91	22.76
			31.5	-3.44	-8.59	22.06
			34	-3.13	-8.66	21.98
			36.5	-3.02	-7.98	22.69
			39	-2.86	-9.15	21.48
41.5	-2.33	-8.92	21.72			
44	-2.48	-8.46	22.18			