7-2016

Reconstructing the Paleoecology and Biogeography of Rhinoceroses (Mammalia: Rhinocerotidae) in the Great Plains of North America, Leading Up to Their Extinction in the Early Pliocene

Bian Wang
University of Nebraska-Lincoln, bian.wang@huskers.unl.edu

Wang, Bian, "Reconstructing the Paleoecology and Biogeography of Rhinoceroses (Mammalia: Rhinocerotidae) in the Great Plains of North America, Leading Up to Their Extinction in the Early Pliocene" (2016). *Dissertations & Theses in Earth and Atmospheric Sciences.* Paper 85.
http://digitalcommons.unl.edu/geoscidiss/85

RECONSTRUCTING THE PALEOECOLOGY AND BIOGEOGRAPHY OF RHINOCEROSES (MAMMALIA: RHINOCEROTIDAE) IN THE GREAT PLAINS OF NORTH AMERICA, LEADING UP TO THEIR EXTINCTION IN THE EARLY PLIOCENE

by

Bian Wang

A THESIS

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Master of Science

Major: Earth and Atmospheric Sciences

Under the Supervision of Professor Ross Secord

Lincoln, Nebraska

July, 2016

RECONSTRUCTING THE PALEOECOLOGY AND BIOGEOGRAPHY OF RHINOCEROSES (MAMMALIA: RHINOCEROTIDAE) IN THE GREAT PLAINS OF NORTH AMERICA, LEADING UP TO THEIR EXTINCTION IN THE EARLY PLIOCENE

Bian Wang, M.S.
University of Nebraska, 2016

Advisor: Ross Secord

Members of the family Rhinocerotidae first appeared in the middle Eocene and were one of most successful mammal groups of the Oligocene and Miocene in North America. Their extinction in the early Pliocene has been attributed to several causes, including cooling climate, an expansion of C_4 grasslands, and faunal turnover favoring high-crowned, open habitat-adapted mammalian taxa. This study tests whether the extinction of North American rhinoceroses in the Great Plains was abrupt or gradual by examining changes in their paleogeographic distribution in a series of time-slices through the Barstovian, Clarendonian, and Hemphillian North American land-mammal ages. It further examines body size changes in rhinoceroses in the late Miocene through early Pliocene epochs, and uses stable isotope data to test whether or not rhinoceroses were able to adapt to the expansion of C_4 grasslands in the late Miocene of the Great Plains.

Results indicate that rhinoceros abundance and geographic distribution remained fairly stable through the Miocene until the late Hemphillian when a rapid decline in abundance occurred, based on data compiled from museum collections and online databases. The decline corresponds closely with the expansion of C_4 grasslands in the Great Plains. Stable carbon isotopes from the tooth enamel of the two most common

rhinoceros Miocene genera, *Aphelops* and *Teleoceras*, indicate that both remained almost exclusively C_3 feeders during the C_4 expansion.

Measurements from lower cheek teeth, used as proxies for body mass, indicate significant increases in size in both *Aphelops* and *Teleoceras* from the Barstovian to Hemphillian. The increase is greater in *Aphelops* than in *Teleoceras*. In the late Hemphillian, however, body size increase in *Aphelops* remained static and decreased slightly in *Teleoceras*. This may be a result of lowered C_3 biomass as C_4 vegetation replaced C_3 plants. This study suggests that the expansion of C_4 grasslands and the failure of rhinoceroses to incorporate C_4 vegetation into their diets, were primary causes of rhinoceros extinction.

Rhinoceros tooth enamel $\delta^{18}O$ values generated for this study decrease latitudinally, indicating a strong latitudinal $\delta^{18}O$ gradient, probably reflecting a latitudinal temperature gradient. This suggests that these large herbivores effectively tracked $\delta^{18}O$ values in environmental water and are potentially useful for paleoclimate reconstructions.

ACKNOWLEDGEMENTS

I would like to thank many people for making my experience as a graduate student at the University of Nebraska-Lincoln truly inspiring and rewarding. I first thank my advisor, Dr. Ross Secord, and committee members, Dr. Jason Head and Dr. David Watkins, for their guidance and constructive contributions to this research and for setting examples of great mentorship and academic excellence.

Thanks to the staff in the Vertebrate Paleontology division of the University of Nebraska State Museum, Dr. Robert Hunt, George Corner, Robert Skolnick, Carrie Herbal, Shane Tucker, and Gail Littrell, for assistance with fossil collections and helpful discussions.

I also thank the following individuals and institutions for providing access museum collections and for help with selecting fossil specimens for isotopic sampling: Alana Gishlick, Judy Galkin, and Dr. Jin Meng in the American Museum of Natural History; Dr. Desui Miao, Dr. Christopher Beard, and Dr. Josh Schmerge in the University of Kansas Natural History Museum; and Dr. Adam Rountry in the University of Michigan Museum of Paleontology. Thanks to Lora Wingate in the University of Michigan Stable Isotope Laboratory for assistance with isotopic analysis. This study could not have been completed without the generosity of these institutions and the efforts of these individuals.

I thank Dr. David Loope and Dr. Patricia Freeman for providing valuable field and practical experience. Thanks to the other faculty and staff of the Earth and Atmospheric Sciences department for their assistance: Dr. Sherri Fritz, Dr. David

Harwood, Dr. Leilani Arthurs, Dr. Tracy Frank, Dr. Clint Rowe, Tina Schinstock, Janelle Gerry, Bryan Miller, and Karl Baumgarten.

Thanks to my lab mates and fellow graduate students for their friendship and support: Evan Whiting, Willow Nguy, John Jacisin, Hannah Darcy, Tom Baldvins, Katheryn Chen, Jon Wallace, Mingyu Yang, Shamar Chin, and Abraham Torres.

Finally, I am grateful to Dr. William S. Bartels in Albion College for guiding me into the profession of vertebrate paleontology and for all of his encouragements.

GRANT INFORMATION

Funding for this project was provided by Friends of the University of Nebraska State Museum, the Nebraska Geological Society and the American Association of Petroleum Geologists (Yatkola-Edwards Student Research Grant), the Department of Earth and Atmospheric Sciences at the University of Nebraska-Lincoln, the National Science Foundation (NSF EAR 1325552 to Dr. Ross Secord), and University of Nebraska State Museum endowments administered through Dr. Secord.

TABLE OF CONTENTS

PREFACE

LIST OF FIGURES

LIST OF TABLES

1. INTRODUCTION

The Rhinocerotidae has a long evolutionary history in the Cenozoic of North America spanning over 40 million years from the middle Eocene to the early Pliocene, and were some of the most ecologically diverse and widespread large herbivores on the continent (Prothero, 1993, 2005). Although there have been several reports of isolated rhinoceros teeth of Blancan age in recent decades (i.e. Madden and Dalquest, 1990; Gustafson, 2012; Farlow et al., 2001; Prothero and Manning, 1987; but also see Martin et al., 2002), it is widely accepted that *Aphelops* and *Teleoceras* were extinct in North America, along with many other land mammals, by the end of the Hemphillian North American land-mammal age (NALMA) (Bell et al, 2004; Prothero, 2005) at approximately 4.7 Ma, and the last appearance of rhinoceroses has traditionally been considered an important datum for the Hemphillian North American land-mammal age (Wood et al., 1941; Tedford et al., 2004).

Peraceras, Aphelops, and *Teleoceras* were the last rhinoceroses known in North America (Matthew, 1932; Wood et al., 1941; Simpson, 1945). All three genera first appeared during the Hemingfordian NALMA about 17.5 million years ago (Ma) (Tedford et al., 2004). *Peraceras* is usually found in lesser abundance than *Aphelops* and *Teleoceras* (Prothero, 2005), and were extinct by the medial Clarendonian NALMA while the other two survived until the Hemphillian (Tedford et al., 2004). Consequently, *Peraceras* is the least well-studied of the three genera (Mead, 1999; Prothero, 2005).

Much of the later history of North American rhinoceroses is recorded in the Neogene deposits of Nebraska and the surrounding Great Plains (Mead, 1999). This area possesses one of the longest and most continuous Cenozoic terrestrial geological sequences in the world, recording some 36 million years of Earth history (Voorhies, 1983; Schultz et al., 1961; Diffendal and Voorhies, 1994). *Aphelops* and *Teleoceras* are a common component of the Barstovian, Clarendonian, and Hemphillian NALMAs of the Great Plains (Mead 2000). *Teleoceras* has been found in nearly all well-sampled Great Plains fossil localities of late Clarendonian and early Hemphillian age, and has also generated much scientific interest because of its peculiar hippopotamus-like body form, suggesting that it had an aquatic lifestyle (see Prothero, 2005 for review).

A global expansion of C_4 biomass between 8 to 3 Ma has been documented in a variety of stable carbon isotope proxies (e.g. Cerling et al., 1993, 1997; Wang et al., 1994; MacFadden and Cerling, 1996; Latorre et al., 1997; Passey et al., 2002; Fox and Koch, 2004; Edwards et al., 2010). In North America, C_4 expansion began in the late Miocene at about 6.5 Ma and continued into the Pliocene (Cerling et al., 1993; Wang et al., 1994; MacFadden and Cerling, 1996; Cerling et al., 1997; Passey et al., 2002; Fox and Koch, 2004). The late Neogene also saw a period of worldwide faunal change (Cerling et al., 1997). Many woodland-adapted mammals transitioned to more open-habitat representatives, and the proportion of high-crowned taxa increased as many low-crowned taxa became extinct (Barry, 1995; Leakey et al., 1996; Cerling et al., 1997; Janis et al., 2000, 2002, 2004). Evolution of high-crowned teeth was not synchronous with the expansion of C_4 grasslands (Strömberg, 2006), however, and appears to be more related to habitat openness and aridity than to grass consumption (Mendoza and Palmqvist, 2008;

Eronen et al., 2009; Strömberg, 2011). Extensive cooling after the Mid-Miocene Climatic Optimum (MMCO, 17 to 15 Ma) is documented in marine records (Fig. 1B) (Zachos et al., 2001, 2008). Cooling climate and expanding C_4 grasslands would have added ecological stress to many herbivorous mammals, forcing them to adapt to new niches or perish.

The extinction of North American rhinos, along with many other land mammals, was presumably driven by climatic and environmental changes in the late Neogene; however, few studies have specifically tested the connection between the extinction of rhinoceroses with these changes. Reconstructing the paleoecology of this once successful mammalian clade in the late Neogene is critical for understanding the factors that led to this demise.

In this study, I focus on the fossil record of *Aphelops* and *Teleoceras* from the Great Plains localities of Barstovian, Clarendonian, and Hemphillian age (ca. 16.0-4.7 Ma; Fig. 1A). I utilize online databases of fossil occurrence data, quantitative methods, and stable isotope geochemistry to examine three aspects of the paleoecology of these rhinos: paleogeoraphic distribution and abundance, body size change, and diet, respectively. I address the following sets of questions: (1) When did rhinoceroses in the Great Plains start to decline in abundance? Was the extinction of rhinoceroses gradual or abrupt? Was it geographically synchronous or diachronous? (2) Were there patterns in body size change in rhinoceroses that might follow changes in climate or environment? (3) Were rhinoceroses able to incorporate C_4 vegetation into their diet or did they remain primarily C_3 consumers?

2. BACKGROUND

2.1 Previous interpretations of paleoecology in *Aphelops* and *Teleoceras*

Aphelops and *Teleoceras* were sympatric rhinos often found in the same fossil localities but exhibited a number of different morphological features. *Aphelops* spp. were hornless aceratherine rhinos. They retained the narrow skull and long-limbed skeletal proportions of earlier rhinocerotids, and are readily distinguished from the horned, broad-skulled, and short-limbed *Teleoceras* spp. The retraction of the nasal notch in *Aphelops* skulls are interpreted to indicate that these rhinos developed a long proboscis or prehensile lip useful for grasping and manipulating leaves and twigs. *Aphelops* spp. were also less hypsodont than *Teleoceras* spp. These lines of evidence have been used to argue that *Aphelops* was a browser and *Teleoceras* a grazer, and explain why these relatively large-bodied herbivores can successfully co-exist in the same areas (Prothero, 1993, 2005).

Siliceous grass remains were found in the oral cavities and rib cages of articulated *Teleoceras major* skeletons at Ashfall Fossil Beds State Historical Park, Nebraska. This suggests that grass was a principle component in the diet of *T. major* (Voorhies and Thomasson, 1979), supporting the interpretation that *Teleoceras* was a grazer. Stable carbon isotope data from rhinoceros tooth enamel confirm a primarily C_3 diet in both *Aphelops* and *Teleoceras* in Florida (MacFadden, 1998) and the Great Plains (Kita et al., 2014) up to the late early Hemphillian (Hh2 biochron). In the Great Plains study, *Teleoceras* exhibited higher mean carbon isotope values than *Aphelops,* plotting in the range expected for open habitat C_3 grazing. In Florida, *Aphelops* remained a C_3 feeder until the latest Hemphillian (Hh4 biochron) when *Teleoceras* shifted to a mixed C_3/C_4 diet, indicating differentiated feeding ecology and niches after the spread of C_4 grasses (MacFadden 1998). Isotope, microwear, and mesowear studies of these taxa from the late Hemphillian of the Great Plains are lacking, however, and it is not clear whether *Aphelops* consumed C_3 browse or C_3 grass.

Teleoceras spp. possess a mixture of characteristics and adaptations that make it one of the most interesting North American rhinos. As Gregory (1942) has pointed out, the hypsodont teeth of *Teleoceras* violate the general correlation of high-crowned teeth with cursorial limb structure in ungulates. Cope (1879) first observed that the body form of *Teleoceras* resembled that of the modern hippopotamus. Based on this similarity, Osborn (1898a, 1898b) suggested that *Teleoceras* lived in large herds and had a lifestyle similar to that of hippos. This interpretation was followed by many subsequent authors and remained popular for more than a century (e.g. Scott 1913; Webb 1983; Voorhies 1981, 1985; Prothero et al. 1989; Prothero 1992, 1993, 1998; Webb & Opdyke 1995; Wall & Heinbaugh 1999). Other similarities have been found between *T. major* assemblage at Ashfall fossil beds and modern hippos, including: (1) apparent herd structure and inferred seasonal breeding (Voorhies 1985), (2) breeding-age sex ratio and community structure (Mead, 2000), and (3) locomotion, inferred from relative limb-segment lengths (Mead, 2000) and tibia/femur ratios (Howell 1965).

The hippo analogy has not withstood some other investigations, such as stable oxygen isotope studies and demography studies. Stable $\delta^{18}O$ values in *Teleoceras* tooth enamel were found to be inconsistent with what would be expected in aquatic mammals.

δ^{18}O values in semi-aquatic hippo ecomorphs are expected to be significantly lower than those of the contemporaneous terrestrial fauna (Clementz et al., 2008) but values in *Teleoceras* were similar to those of the associated Ashfall mammals (Clementz et al., 2008) and to coexisting *Aphelops* (MacFadden, 1998). MacFadden (1998) suggested that good modern analogs for *Aphelops* and *Teleoceras* may be the terrestrial browsing black rhino (*Diceros bicornis*) and the terrestrial grazing white rhino (*Ceratotherium simum*), respectively, based on stable carbon and oxygen isotope values from their tooth enamel. Additionally, Mihlbachler (2003, 2005) found a disproportionately elevated young-male mortality rate in a *Teleoceras proterum* death assemblage, suggesting a socially-mediated, age-specific mortality rate unlike that of the modern hippos but similar to that of the modern black rhino.

2.2 Estimating the body size of fossil rhinoceroses

Body size is one of the most important ecological characteristics in biology and paleobiology, providing crucial ecological implications for diet, population density, physiology, behavioral adaptations, life history traits, and biogeography (Calder, 1984; Peters, 1983). Of direct relevance to this study, body size of mammalian herbivores has implications for the minimum quality of food necessary for survival (Bell, 1971; Jarman, 1974; Geist, 1974), as gut volume scales isometrically with body mass ($BM^{1.0}$) while metabolism is a fractional power of body mass ($BM^{0.75}$). Hence larger herbivores have a greater capacity to process and survive on poor quality (high fiber) forages (Demment and Van Soest, 1985). More recent studies have attributed the tolerance of less nutritious plants to a higher scaling exponent of food intake in larger herbivores, rather than increased digestive efficiency (e.g., Müller et al., 2013). Nonetheless, the relationship between body mass and herbivore feeding ecology is a fundamental principle and has been applied to understanding the ecology of ungulates of African savannahs. In agreement with this relationship, the extant grazing white rhinoceros (*Ceratotherium simum*) has body mass ranging from 1400kg to 2300kg, while the sympatric, browsing black rhinoceros (*Diceros bicornis*) has body mass ranging from 816kg to 1300kg (Silva and Downing, 1995; Owen-Smith, 1988).

Another advantage of larger body size is more efficient thermoregulation. Approximately 65 to 75% of extant mammals and birds are generally smaller-bodied at lower latitudes (Blackburn et al. 1999, Mayr, 1963; Ashton et al. 2000, Rodríguez et al. 2008). This relationship, known as “Bergmann’s Rule”, is usually attributed to temperature and/or primary productivity. Larger animals have a greater surface area-to-volume ratio and therefore retain more heat than smaller animals, so large body size may be adaptive for colder climates (Gardner et al. 2011). Temperature may also indirectly affect body size by controlling the distribution of plants and growing season length (McNab, 2010; Peñuelas and Filella 2001). In general agreement with Bergmann’s Rule, significant decreases in body mass have been found in a variety of fossil taxa associated with warming during the Paleocene-Eocene Thermal Maximum (PETM), followed by post-PETM increases in body mass when the temperature cooled (Secord et al., 2012).

An increase in the body mass of *Aphelops* in the late Neogene was reported by Prothero and Manning (1987). Based on the marine record (Zachos et al 2001, 2008), there was a decrease in global temperature of ~4°C from the MMCO to the early Pliocene

(Fig. 1B). Although the increase in *Aphelops* body mass could be related to temperature change, a more rigorous quantification of numerous mammalian lineages is needed before any strong conclusions can be made.

When estimating body size of fossil rhinoceroses, it is important to minimize possible bias introduced by sexual dimorphism. Sexual dimorphism in *Teleoceras* has been studied by many authors before, both qualitatively (e.g., Osborn, 1898a, 1904; Voorhies and Stover, 1978) and quantitatively (e.g., Voorhies, 1990; Bales, 1995; Mead, 2000; Mihlbachler, 2005; Prothero and Manning, 1987; Prothero, 2005). Other than the clearly dimorphic lower tusk (i2), the significance and degree of sexual dimorphism in dental and postcranial measurements vary among different studies. Late Miocene Great Plains populations appear to have been more dimorphic than Florida populations (Mihlbachler 2005). Although less well-studied, sexual dimorphism in *Aphelops* (*A. mutilus*) has also been reported (Matthew, 1932; Lambert, 1994; Mihlbachler, 2005).

In this study, I use the size of lower cheek teeth to infer body size change in rhinoceroses. First lower molar (m1) area is strongly correlated with body mass in extant medium and large herbivores (e.g., Damuth, 1990). Lower cheek tooth lengths are also commonly used and may be a more reliable proxy (Damuth and MacFadden, 1990; Janis, 1990). Several things make teeth a good proxy for body mass estimation: (1) they are the hardest mineralized tissues in animals' body and are abundant in the fossil record; (2) they are somewhat rectangular shape, making measurements easy to standardize and reproduce; (3) the lengths of m1 have been found to be the least sexually dimorphic among 45 craniodental and postcranial characters in the *Teleoceras major* from Ashfall, with a male-female ratio of 1.01, while limb measurements are highly sexually dimorphic, with males larger by 20-29% (Mead, 2000).

2.3 Carbon Isotopes in Mammalian Diet

Mammalian herbivore tooth enamel reliably records the isotopic composition of ingested plants with predicable enrichment (Lee-Thorp and van der Merwe, 1987; Cerling and Harris, 1999; Passey et al., 2005). Atmospheric CO_2 is fixed into plants with varying degrees of fractionation due to different photosynthetic pathways. Three pathways are used: C_3, CAM (crassulacean acid metabolism), and C_4. Resulting $\delta^{13}C$ values are lowest in C_3 plants (-37‰ to -21‰), intermediate in CAM plants, and highest in C_4 plants (-19‰ to -9‰) (O'Leary, 1988; Cerling and Ehleringer 2000).

Mammalian herbivore tooth enamel bioapatites are enriched in $\delta^{13}C$ relative to bulk diet because both metabolism and biomineralization fractionate ingested carbon. The CO_3 component of tooth enamel therefore reflects the carbon isotope composition of the ingested plants, and mammals feeding on C_3 vegetation can be readily distinguished from those consuming C_4 plants, or those that have mixed C_3/C_4 diets. Pure C_3 and C_4 consumers have non-overlapping ranges, while mammals with mixed C_3/C_4 diets will have intermediate $\delta^{13}C$ values (MacFadden and Cerling, 1996; Cerling et al., 1997, 1998; Koch, 1998; MacFadden et al., 1999). Plants using the CAM photosynthetic pathway, characteristic of succulents, have intermediate values overlapping with those of C_3 and C_4 vegetation (O'Leary, 1988; Ehleringer et al., 1991). CAM plants are not widespread

(Ehleringer et al., 1991), however, and are not typically consumed by ungulates. Therefore, they are not considered further in this study.

Isotopic variability in C_3 plants is generally greater than that in C_4 plants and is caused primarily by differences in water availability and light intensity, and to a lesser extent by temperature and nutrient availability (O'Leary et al., 1992). In general, $\delta^{13}C$ values increase from denser and wetter forested parts of an ecosystem to more open or drier habitats (Ehleringer et al., 1986; Stewart et al., 1995; Heaton, 1999; Diefendorf et al., 2010; Kohn, 2010). These trends are reflected in the carbon isotope compositions of tooth enamel ($\delta^{13}C_E$) of herbivorous mammals: higher values are representative of more open, drier habitats and low values more closed, wetter habitats (O'Leary et al., 1992; Koch, 1998; Cerling and Harris, 1999; Feranec, 2003, 2007; Feranec and MacFadden, 2006; Secord et al., 2008).

Resource partitioning in diet and habitat use may be revealed through stable isotope analysis (Koch et al., 1998; Balasse et al., 2003; Feranec and MacFadden, 2006), and has been studied in both modern and ancient environments where a mixture of C_3 and C_4 plants is present (e.g. Wang et al., 1994; MacFadden and Cerling, 1996; Koch, 1998; Feranec and MacFadden, 2006).

2.4 Oxygen Isotopes in Tooth Enamel

The oxygen isotope composition of mammalian tooth enamel can be useful for understanding the animals’ drinking behavior and habitat preference, as well as local climatic conditions (Kohn, 1996; Kohn et al., 1996; Levin et al., 2006; Secord et al., 2008, 2010, 2012; Zanazzi and Kohn, 2008; Tütken and Vennemann, 2009). The oxygen isotopic composition of mammalian tissues is determined by the composition of a mammal's body water and temperature at the time of apatite formation. Body temperature is generally constant in mammals. The oxygen composition of body water depends on the oxygen composition of water ingested from drinking and from food, and the animal's physiology (Bryant and Froelich, 1995; Land et al., 1980; Longinelli, 1984; Luz and Kolodny, 1985; Kohn, 1996; Kohn et al., 1996, 1998). Water from both sources is ultimately derived from precipitation, but leaf water tends to be ^{18}O-enriched due to evaporation, and enrichment increases with increasing aridity or solar radiation (Yakir et al., 1990; Yakir, 1992). Therefore, taxa that are frequent or obligate drinkers should have lower $\delta^{18}O_E$ values more reflective of local drinking water than taxa that derive a significant proportion of water from leaves (Bryant and Froelich, 1995; Kohn, 1996 Balasse et al., 2003; Levin et al., 2006).

Species that have physiological adaptations for retaining water in arid regions and/or get a large part of their water from plants are expected to have high $\delta^{18}O_E$ values relative to water-dependent species that rely heavily on drinking. In contrast, large semi-aquatic herbivores, such as hippopotami, are expected to have the lowest $\delta^{18}O_E$ values in a contemporaneous fauna (Clementz et al., 2008). Water-dependent herbivores that rely on drinking and consume vegetation in areas where water is readily available to plants should have low to intermediate values. Thus, a comparison of mean $\delta^{18}O_E$ values within a fauna to those of individual species can be used to infer water dependence (e.g., Levin et al., 2006). Another factor to consider is the tendency for the leaf water in C_4 grasses to be more ^{18}O-enriched than leaf water in C_3 grasses, with a higher difference (~5‰) under low relative humidity growth conditions and a lower difference (~1‰) at high humidity (Kohn, 1996; Helliker and Ehleringer, 2002).

Mammalian $\delta^{18}O_E$ values can also be useful for making paleoclimate interpretations (e.g., Fricke and O'Neil, 1999; Secord et al., 2010, 2012). The composition of surface water is ultimately controlled by the composition of precipitation, although surface water reservoirs can vary substantially due to differing histories (e.g., Dutton et al., 2005).

The $\delta^{18}O$ values of precipitation are affected primarily by temperature at mid- to high-latitudes and by vapor source and vapor transport (Dansgaard, 1964; Rozanski et al., 1992; Gat, 1996). Warmer temperatures generally result in more positive $\delta^{18}O$ values in precipitation and cooler temperatures more negative ones due to Rayleigh fractionation and local atmospheric temperature at the time of precipitation (Sharp, 2007). Thus, warming and cooling trends in the geologic record are expected to positively covary with $\delta^{18}O$ values in precipitation, assuming no changes in vapor source or strong influences from other sources (e.g., Fricke and O'Neil, 1999; Koch et al, 2003; Kohn and Welker, 2005; Secord et al., 2010). In turn, large scale changes in the $\delta^{18}O$ value of meteoric water should be reflected in surface water consumed by mammals (Fricke and O'Neil, 1996; Iacumin and Longinelli, 2002; Balasse et al., 2003; Secord et al., 2010, 2012).

3. MATERIALS AND METHODS

3.1 Paleogeography

Faunal lists were compiled from the Miocene Mapping Project database (MioMap; Carrasco et al., 2005) and Fossilworks (formerly the Paleobiology Database) for fossil localities correlated to the Barstovian, Clarendonian, and Hemphillian land mammal ages in South Dakota, Nebraska, eastern Colorado (east of 105°W), Kansas, Oklahoma, and northwestern Texas (approximately north of 32°N and west of 99°W). Base map of geologic formations is obtained from the U.S. Geological Survey.

Because the number of rhino specimens for each time interval will covary with the number of localities sampled, I calculated the relative abundance of rhinoceros specimens as a percentage of the number of localities:

$$\text{Abundance (\%)} = \frac{\text{Number of localities that contain rhinoceroses}}{\text{Total number of localities}} * 100\%$$

Only localities that produced medium to large herbivores (e.g. Artiodactyls, Perissodactyls, Proboscideans) were included in the analysis to avoid localities with a sampling bias for small size. Ideally, abundance would be calculated relative to the total number of identified specimens or the total number of individuals in each fauna but these data were not available for most localities.

Localities were subdivided into biochrons using age constraints given in MioMap and definitions by faunal succession from Tedford et al. (2004). Land-mammal ages are biochronologic units based on the age and succession of mammalian evolutionary events (Lindsay, 2003). In practice, many NALMAs are defined on the basis of immigrant taxa. Boundaries and subdivisions are established at first appearance datums and evolutionary events loosely tied to stratal succession (Wood et al., 1941; Woodburne, 2004). When zonal boundaries in a lithological unit do not directly correspond to chronal boundaries and a locality in this lithological unit only produces range-through taxa, it is not possible to constrain its chronological age. This problem resulted in a number of localities that could not be assigned to a specific biochron. Most of these localities were Clarendonian. The majority of Clarendonian fossil localities are in Nebraska, yet many of the lithological units and faunas in Nebraska cross the Cl2 - Cl3 boundary (e.g. Merritt Dam Member of Ash Hollow Formation, Snake Creek Fauna; see Tedford et al., 2004). Therefore, Cl2 and Cl3 localities were grouped for analysis.

3.2 Body Size Change

Lower cheek teeth measurements were taken from a total of 82 *Aphelops* and 183 *Teleoceras* specimens in collections at the American Museum of Natural History (AMNH), the University of Nebraska State Museum (UNSM), and the University of Kansas Natural History Museum (KUVP). Specimens from the Great Plains were from localities spanning the Ba1 through Hh3 biochrons. The maximum length and width of each tooth were measured with a digital caliper. Composite measurements (m1 area and m1-3 length) were calculated from the measured dimensions of individual teeth. Only one element in a pair (left or right) was measured.

Estimates of body mass were made using three parameters: length of the first molar (m1L), area of the first molar (m1A), and length of the molar tooth row (m1-3L). Body mass was calculated using Damuth's (1990) equations for non-selenodont ungulates and Janis' (1990) equations for perissodactyls and hyracoids.

Measurements were grouped by biochron and NALMA for statistical analyses based on age of the localities. Cl2 and Cl3 biochrons are grouped for all analyses due to the lack of precision in dating. Statistical comparisons were made between the biochron groups as well as between the NALMA groups. No *Aphelops* specimen was measured from Cl1, but because Cl1 was a relatively short time interval (~0.5 m.y.), the Ba2 and Cl2-3 groups were compared instead.

To examine body mass change through time I tested for the difference between tooth measurements for subsequent time intervals using Student's *t*-test. To compare body mass differences between *Aphelops* and *Teleoceras*, generated from the three body mass proxies, I used Student's *t*-test.

3.3 Isotopic sampling and statistical analysis

Tooth enamel samples from 38 *Teleoceras* specimens and 22 *Aphelops* specimens in AMNH, UNSM, and KUVP collections were bulk sampled. To increase the number of horse samples from the poorly represented late Hemphillian, three horse teeth were also bulk sampled. All specimens sampled were from Hemphillian localities in the Great Plains (Fig. 2). Preference was given to sampling last molars and premolars (m3 and p4, respectively) to avoid a weaning signal, because these teeth in most horses erupt ontogenetically late. However, due to the small number of fossils from some localities and the limited number of museum specimens available for sampling, several m2s were included as well.

Approximately 4mg of pristine enamel powder was drilled from surfaces parallel to the growth axis of the teeth using a 1 mm diamond bit and a variable speed dental drill. Pretreatment method followed Koch et al. (1997) with the exception of drying by lyophilization. Samples were treated with 3% reagent grade NaOCl for 24 hours to remove organic matter and with 1 M buffered acetic acid for 24 hours to remove nonstructural carbonate. Each treatment was followed by centrifuging and rinsing five times with deionized water. Samples were dried overnight in a drying oven at 60°C.

Isotopic measurements were done at the University of Michigan Stable Isotope Laboratory (UMSIL). Samples were reacted at 77° ± 1°C with anhydrous phosphoric acid for 8 minutes in a Finnigan MAT Kiel IV preparation device. Isotopic ratios of the resultant CO_2 were coupled directly to the inlet of a Finnigan MAT 253 triple collector isotope ratio mass spectrometer. Analytical precision at UMSIL is better than ±0.1‰ (1 standard deviation) for both $\delta^{18}O$ and $\delta^{13}C$ values, based on international standards for carbonate (NBS-18, NBS-19). Intra-lab enamel standards (LOX, from the African elephant; MES-1, from fossil mammoth enamel) were used to monitor variance among batches. Mean values and variances were: $\delta^{18}O = 31.80 \pm 0.13$‰ and $\delta^{13}C = -5.69 \pm 0.02$‰ (95% confidence, n=9) for LOX and $\delta^{18}O=22.87\pm0.08$‰ and $\delta^{13}C = -9.70 \pm 0.04$‰ (95% confidence, n=9) for MES-1 (error reports as 1 standard deviation).

Isotopic results are expressed in standard δ-notation: $X = [(R_{sample} / R_{standard}) - 1] \times 1000$, where X is the $\delta^{13}C$ or $\delta^{18}O$ value, and $R = {}^{13}C / {}^{12}C$ or ${}^{18}O / {}^{16}O$, respectively. The $\delta^{13}C$ values are reported relative to the Vienna PeeDee Belemnite (VPDB) standard and $\delta^{18}O$ values are reported relative to the Vienna Standard Mean Ocean Water (VSMOW) standard.

Because sample sizes were relatively small in some cases, I relied on non-parametric analysis (Mann-Whitney *U* test) to test for difference in $\delta^{13}C$ and $\delta^{18}O$ values between *Aphelops* and *Teleoceras*. Comparisons were done for each biochron, as well as for each locality in which they co-occurred in order to tease out the influence of spatial and temporal differences.

Using latitudinal data for fossil localities from MioMap, I calculated the relationship between latitude and $\delta^{13}C_E$ and $\delta^{18}O_E$ values using reduced major axis regression. Given the limited longitudinal coverage of my sampled localities, I do not expect significant trends in $\delta^{13}C_E$ and $\delta^{18}O_E$ values with longitude.

3.4 Predicting carbon isotope values for late Neogene herbivores

I follow the model developed by Kita et al. (2014) to predict expected $\delta^{13}C$ values in rhino and horse tooth enamel for a variety of late Neogene biomes. The model uses values for modern vegetation normalized to parameters for the late Neogene of Nebraska, including the effects of latitude and altitude on $\delta^{13}C$ values in modern vegetation, and changes in the composition of atmospheric CO_2 between the late Neogene and present. A diet-enamel enrichment factor for ungulates of 14.1 ± 0.5‰ (1 S.D.) is also incorporated following Cerling and Harris (1999). Model results indicate the following boundaries and ranges for mean $\delta^{13}C_E$ faunal values: closed canopy forest (rainforest and monsoon forest): ≤−12.1‰; open canopy biomes ("dry" and "wet" woodland-savanna, "dry" woody scrubland, "dry" forest, and "dry" C_3 grassland): >−12.1‰ to −7.7‰; mixed C_3/C_4 biomes: >−7.7‰to 2.1‰; and pure C_4 grasslands: ≥2.1‰.

4. RESULTS

4.1 Paleogeography

Numbers of localities and relative abundance of *Aphelops* and *Teleoceras* in the Barstovian, Clarendonian, and Hemphillian land-mammal ages are reported in Fig. 3. Range maps are presented in Fig. 4-6.

The abundance of *Teleoceras* by percent localities showed a progressive increase from 34% in the Barstovian to 42% in the Clarendonian and ultimately 52% in the Hemphillian (Fig. 3). The abundance of *Aphelops* showed a decrease from 21% in the Barstovian to 12% in the Clarendonian, followed by a prominent increase to 37% in the Hemphillian. *Aphelops* is noticeably less abundant than *Teleoceras* in all three land mammal ages. Overall, localities that contained these two rhinos increased in frequency, suggesting that these rhinos, especially *Teleoceras*, became progressively more abundant from the Barstovian to the Hemphillian.

Barstovian localities are restricted to Nebraska and northeastern Colorado (Fig. 4), while Clarendonian and Hemphillian localities cover larger areas of the Great Plains (Fig. 5-6). In all of the land-mammal ages, rhinoceros localities covered approximately the same amount of geographic area as did all fossil localities. Calculated abundances, therefore, are less a measure of how widespread rhinos were, but rather are more informative about the relatively density of rhino populations.

Numbers of localities by biochron groups are reported in Table 1. A small number of Hemphillian localities lacked information needed for biochron assignments. Calculated abundance at the biochron level using well-dated localities are plotted in Fig. 7. Abundances of *Teleoceras* decreased from 42% in Ba1 to 32% in Ba2 but rapidly recovered in the Clarendonian and remained approximately 60% until Hh1. Abundances of *Aphelops* also decreased from Ba1 (38%) to Ba2 (15%), remained relatively low in the Clarendonian, and rose to 30% in Hh1. The most compelling pattern is found in the Hemphillian. Both rhinos increased in abundance from Hh1 to Hh2, but exhibit huge decreases from Hh2 to Hh4. The decline was rather rapid in *Teleoceras*, from 79% in Hh2 to 30% in Hh3. In *Aphelops* the greatest decline in abundance was from 53% in Hh3 to 22% in Hh4. Noticeably, *Aphelops* is less abundant than *Teleoceras* in all biochrons except Hh3.

This general pattern persists when less well-dated localities are incorporated (by using maximum possible numbers of localities in a biochron, or by dividing numbers of uncertain localities evenly into possible biochrons), although specific percent abundances change slightly. These results show that the decline of *Aphelops* and *Teleoceras* in the Great Plains occurred later than Hh2 (7.5-6.7 Ma). At the onset of the decline, *Teleoceras* seems to have been affected more strongly than *Aphelops*, resulting in a brief interval of lower abundance in Hh3 (6.7-5.9 Ma).

The pattern of decline is largely a function of the data from Texas, which comprise the majority of Hemphillian localities. There is a paucity of fossil localities from the latest Hemphillian (Hh4; Fig. 8), and rhinoceroses are only found in three of the eleven Texas localities and one out of five Oklahoma localities, but are found in both of the Nebraska localities.

4.2 Body Size Change

4.2.1 Tooth measurements of *Aphelops*

Tables 2-3 report descriptive statistics for each measured variable of *Aphelops*. Mean length of m1 increased significantly (p<0.01, t-test; Table 4) from 37.5 ±2.7 mm in the Barstovian to 40.43 ±3.90mm in the Clarendonian and ultimately 53.7 ±3.9 mm in the Hemphillian. Significant increases are also found in m1A and m1-3L measurements (Tables 2, 4) at the NALMA scale.

Two additional patterns can be observed at the biochron scale in *Aphelops* (Fig. 9, Table 3). First, the biggest increase in m1 size occurred between the late Clarendonian (Cl2-Cl3) and the late early Hemphillian (Hh2). Second, from Hh2 to Hh3 the increase in all three proxies have largely stopped and size differences are insignificant (p>0.33, t-test; Table 4).

4.2.2 Tooth measurements of *Teleoceras*

Tables 5-6 report descriptive statistics for each measured variable of *Teleoceras*. Mean m1 lengths and m1 areas remained static from the Barstovian to the Clarendonian (p>0.22, t-test; Table 7) and increased significantly from the Clarendonian to the

Hemphillian (*p*<0.01, *t*-test), while mean m1-3 lengths increased progressively from the Barstovian to the Hemphillian (Table 5).

At the biochron scale, m1 length and m1 area fluctuated from Ba1 to Cl2-3, increased significantly (*p*<0.01, *t*-test) from Cl2-3 to Hh1, while m1-3 length increased steadily from Ba1 to Hh2, with a significant increase from Hh1 to Hh2. All three proxies exhibited a small decrease from Hh2 to Hh3.

4.2.3 *Aphelops* and *Teleoceras*

Body mass estimates using m1 length, m1 area, and m1-3 length are listed in Table 8. Estimates based on m1 length and m1 area derived from equations in Janis (1990) are considerably larger than those derived from Damuth's (1990) equations. Despite the huge difference in body mass estimates, the three proxies show similar trends in body size evolution of the two rhinos. In short, *Aphelops* started out as a much smaller rhino than *Teleoceras* during the Barstovian and the Clarendonian, but surpassed *Teleoceras* in body size in the Hemphillian (Fig. 9, Table 9).

The timing of the changes indicated by the three proxies, however, are slightly different, with m1 length and m1 area suggesting overlapping body sizes in Hh1, and m1-3 length suggesting overlaps in Hh2. This difference probably has to do with the higher rate of increase in m2 and m3 compared to m1 in *Teleoceras* prior to Hh3.

4.3 Stable Isotopes

The distribution of isotope samples by biochron and state are summarized in Table 10. Summary statistics of carbon and oxygen isotope values are listed in Table 11

4.3.1 Carbon Isotopes

No significant correlation exists between latitude and $\delta^{13}C_E$ values (Fig. 10). Regression yields the equation:

$$\delta^{13}C_E = -0.56\ (\pm 0.07) * \text{Latitude} + 12.99(\pm 8.30) \qquad (1)$$
$$(r^2 = 0.02, p=0.26)$$

Individual $\delta^{13}C_E$ values are plotted in Fig. 11. The mean $\delta^{13}C_E$ value of *Teleoceras* in Hh1 is -8.4 ±0.5‰. All *Teleoceras* samples from Hh1 plot in the "dry," water-stressed open canopy $\delta^{13}C_E$ range with a possibility of a small C_4 component. In Hh2 and Hh3, mean $\delta^{13}C_E$ values of *Teleoceras* remained approximately -9.0‰ but have larger ranges (Fig. 12), probably partially due to a bigger sample size. Both Hh2 and Hh3 samples include single individuals showing unequivocal C_4 signals (>-7.7‰) and more negative values in the wet, open canopy C_3 range. A lower mean $\delta^{13}C_E$ values of -10.0±1.0‰ occurs in *Teleoceras* from Hh4 (Fig. 12). No significant difference occurs in *Teleoceras* $\delta^{13}C_E$ values between subsequent biochrons (Table 12).

Aphelops exhibits a wider range of $\delta^{13}C_E$ values than *Teleoceras* (Fig. 11). In Hh2, most *Aphelops* samples fall into the water-stressed C_3 range, like *Teleoceras*, with the exception of one very high $\delta^{13}C_E$ value that plots well into the mixed C_3/C_4 range. This sample from Box T Ranch, Texas, has a $\delta^{13}C_E$ value of -5.9‰, the highest of all rhinos sampled in this study. In Hh3, three *Aphelops* samples plot near the lower boundary of the mixed diet range, two samples plot in the forest/dense vegetation range, while the rest fall in the middle of the open canopy range. Interestingly, the early Hh3 Coffee Ranch of Texas produced one of the relatively high $\delta^{13}C_E$ values (-7.6‰) and one very low $\delta^{13}C_E$ value (-14.9‰), the latter being the lowest value among all rhinos sampled in this study. The second lowest $\delta^{13}C_E$ value (-12.6‰) was collected from the Rick Irwin Site, Nebraska. In Hh4, all sampled *Aphelops* fall in the wet open canopy range. Although mean $\delta^{13}C_E$ values decreased progressively from -8.7±1.5‰ in Hh2 to -10.7±0.7‰ in Hh4 (Fig. 12, Table 11), the changes are not significant (Tables 12).

No significant difference in $\delta^{13}C_E$ values can be found between *Aphelops* and *Teleoceras* in any biochron or any single locality in which they co-occurred (Tables 12, 13). Both rhinos appear to be a primarily C_3 feeders with the capability of incorporating only a small amount of C_4 in their diet. The high $\delta^{13}C_E$ values in most *Aphelops* and *Teleoceras,* with many plotting in the water-stressed C_3 range, suggests that both these rhinos occupied very open habitats, such as dry grasslands.

In contrast, one of the three horses sampled in this study from the Hh4 of Nebraska has a $\delta^{13}C_E$ value of -3.3‰, clearly consuming a large portion of C_4. None of the rhinos yields values this high. The other two horse samples have $\delta^{13}C_E$ values similar to those of the rhinos (-9.9‰ and -10.8‰) (Fig. 11).

4.3.2 Oxygen Isotopes

Mean $\delta^{18}O_E$ values were higher in *Aphelops* than in *Teleoceras* by about 1.5‰ in biochrons Hh2 and Hh3, but were over 2‰ lower in *Aphelops* than in *Teleoceras* in Hh4

(Fig. 14). However, these differences were not statistically significant ($p>0.11$, Mann-Whitney; Table 12). No significant difference in $\delta^{18}O_E$ was found between *Aphelops* and *Teleoceras* in any locality in which they co-occurred, either ($p>0.25$, Mann-Whitney; Table 13).

Teleoceras $\delta^{18}O_E$ values remained static throughout the Hemphillian (Fig. 12, 13; Table 12). In contrast, a large, significant ($p=0.02$, Mann-Whitney) decrease of 4.3‰ in mean $\delta^{18}O_E$ values in *Aphelops* occurred from biochron Hh3 to Hh4 (Fig. 12, Table 12). However, the latitudinal distribution of samples is uneven; seven of the twelve Hh3 *Aphelops* samples are from Texas and only one is from Nebraska, while all Hh4 samples are from northern Nebraska. The difference could therefore be a result of latitudinal difference instead of temporal changes, as $\delta^{18}O$ values in precipitation are expected to be more negative at the higher latitude of northern Nebraska (at a gradient of approximately 1.04‰ per degree latitude, using equation (6) below).

Regression of individual rhinoceros $\delta^{18}O_{Enamel}$ values against latitude yield the equation:

$$\delta^{18}O_E = -1.00\ (\pm 0.08) * \text{Latitude} + 65.30(\pm 11.30) \qquad (2)$$
$$(r^2 = 0.59,\ p<0.001)$$

Regressions using only *Aphelops* samples or *Teleoceras* samples yield the following equations:

$$\textit{Aphelops}\ \delta^{18}O_E = -0.92\ (\pm 0.14) * \text{latitude} + 61.633(\pm 29.00) \qquad (3)$$
$$(r^2 = 0.55,\ p<0.001)$$

$$\textit{Teleoceras}\ \delta^{18}O_E = -1.16\ (\pm 0.12) * \text{latitude} + 71.91\ (\pm 22.34) \qquad (4)$$

$$(r^2 = 0.63, p<0.001)$$

However, two *Aphelops* samples have noticeably low $\delta^{18}O_E$ values (23.1‰ and 24.1‰; Fig. 14A-B) and were identified as outliers by SYSTAT software. These two samples are from the Coffee Ranch locality in Texas and have unusually low and unusually high $\delta^{13}C$ values (Fig. 11), suggesting possible diagenetic alteration of enamel. Excluding these outliers results in a stronger correlation between *Aphelops* $\delta^{18}O_E$ values and latitude:

$$\textit{Aphelops}\ \delta^{18}O_E = -0.94\ (\pm 0.08) * \text{latitude} + 62.834\ (\pm 10.98) \qquad (5)$$
$$(r^2 = 0.85, p<0.001)$$

Similarly, correlation is stronger for all rhinos when the outliers are excluded:

$$\delta^{18}O_E = -1.04\ (\pm 0.07) * \text{latitude} + 67.02(\pm 8.11) \qquad (6)$$
$$(r^2 = 0.74, p<0.001)$$

Regressions for each genus in each biochron are plotted in Fig. 15. Regressions were not made for Hh4 because the only two Hh4 localities are from the same latitude in northern Nebraska. All regressions yield similar relationships between $\delta^{18}O_E$ values and latitude.

5. DISCUSSION

Results indicate that the start of the decline of rhinoceroses in the Great Plains occurred during the Hh3 biochron (6.7-5.9 Ma) with a sharp decrease in the abundance of *Teleoceras*, followed by a large decrease in *Aphelops* abundance in Hh4 (5.9-4.7 Ma) (Fig. 3). The timing of the decline corresponds closely to the spread of C_4 grasses in the Great Plains, which started at approximately 6.5 Ma and continued into the Pliocene (Cerling et al., 1993; Wang et al., 1994; MacFadden and Cerling, 1996; Cerling et al., 1997; Passey et al., 2002; Fox and Koch, 2004). This strongly supports the hypothesis that the extinction of North American rhinoceroses was related to this vegetation change and their failure to adapt to the new food resource.

The shift from a C_3 diet to a mixed C_3/C_4 diet recorded in *Teleoceras* tooth enamel from the latest Hemphillian of Florida led MacFadden (1998) to suggest that the extinction of rhinoceroses may not be a result of diminished C_3 food resources. Both rhinos became extinct even though *Aphelops* was a presumed browsing browser and *Teleoceras* a presumed grazing grazer. Extinction in other mammal groups (such as the horses) were selective (browsers go first) and progressive (Janis et al., 2000, 2002, 2004; MacFadden, 1992).

In contrast, stable carbon isotope values in this study do not indicate a prominent shift to a larger component of C_4 in the diet of *Teleoceras* or *Aphelops* in the Great Plains, showing no evidence of strengthened niche partitioning between the two sympatric rhinos. Both rhinos remained primarily C_3 consumers until the end of their extinction. This does not preclude the possibility of an extinction driven by diminished food resources, at least in the Great Plains.

Today, C_4 vegetation is found in lower abundance in the northern plains than the southern plains (Teeri and Stowe, 1976). Modeling results predict that C_4 vegetation is favored in areas with higher daytime growing season temperature (Cerling et al., 1997). Stable carbon isotope data from fossil horses also suggest that C_4 expansion in the Great Plains occurred earlier at lower latitudes (Cerling et al., 1997; Passey et al., 2002). Results in this study indicate large decreases in *Teleoceras* and *Aphelops* abundance in Hh3 and Hh4, respectively. However, this pattern is driven largely by a large drop in abundance in Texas, while in Nebraska a relatively high abundance of both *Aphelops* in *Teleoceras* sustained from Hh3 to Hh4. Sample sizes are small in Hh4, but nonetheless, the suggested pattern is consistent with an earlier spread of C_4 grasslands in lower latitudes. It is worth testing whether or not this pattern stands when using other abundance metrics, such as species diversity.

At the beginning of C_4 expansion in North America, fossil horses at low latitudes showed considerable variability in $\delta^{13}C_E$ values, indicating reliance on both C_3 and C_4 vegetation possibly during different times of the year (Cerling et al 1997). Similarly, rhino $\delta^{13}C_E$ values in this study show a slightly wider range of values in Hh2 and Hh3 largely represented by samples from Texas. The widest range of values is found in *Aphelops*, the presumed browser, instead of *Teleoceras*, the presumed grazer. Tooth enamel $\delta^{13}C$ values of *Aphelops* samples from the Coffee Ranch of Texas include a value high enough to suggest an unequivocal C_4 component in diet and a value low enough to indicate feeding in a densely vegetated, wet environment. As mentioned above, these specimens both yielded unusually low $\delta^{18}O_E$ values (outliers in Fig. 14, 15), suggesting possible diagenetic alteration. Most $\delta^{13}C_E$ values for both rhinos are consistent with feeding in open, dry environments where plants were undergoing water stress or consuming a mixture of primarily C_3 vegetation, with a small component of C_4. In either of these cases, dry open environments are indicated, which would probably have a sizable component of grasses.

Additionally, some $\delta^{13}C_E$ values in *Aphelops* (and *Teleoceras*) plot in the low end of the range for mixed C_3/C_4, suggesting that it was consuming some C_4 grass. This calls into question past interpretations of exclusive browsing in *Aphelops*, which were not based on microwear studies. Patterns of body size change indicated by the three dental proxies suggest a large increase in the body mass of *Aphelops* from the Barstovian to the Hemphillian. The evolution of larger body size would have enabled *Aphelops* to better maintain body heat and to feed on less nutritious vegetation, such as grasses. This, coupled with more high-crowned teeth in later species of *Aphelops* (Kita et al., 2014; Prothero, 2005), suggest that *Aphelops* potentially shifted from C_3 browsing in the middle Miocene to C_3 grazing in the late Miocene/early Pliocene, or to a mixed diet of graze and browse. This hypothesis is supported by $\delta^{13}C_E$ values in *Aphelops* that plot alongside those of *Teleoceras* in the range expected for dry, water-stress C_3 vegetation (Fig. 11). Browse is likely to be greatly diminished in such dry environments, relative to wetter, more forested habitats.

The earliest unambiguous C_4 dietary signal occurs in *Teleoceras* (and *Cormohipparion*) teeth from Ashfall fossil beds in Nebraska (see Clementz et al. 2008 supplemental file, and Tipple and Pagani, 2007), of early Clarendonian age. This observation, along with the few rhinoceros samples that indicate a C_4 component in this study (Fig. 11), suggest that these rhinos were capable of incorporating a small amount of C_4 in their diet.

The considerably lower $\delta^{13}C_E$ values in Hh4 found here suggest different environmental conditions in Nebraska than in Florida. Distribution of C_4 grasses are correlated with temperature and require precipitation during growing seasons (Teeri and Stowe 1976). Higher precipitation in Florida than in the continental interior potentially contributed to a higher amount of C_4 biomass, allowing *Teleoceras* in Florida to incorporate a larger portion of C_4 in their diet in the latest Hemphillian. A drier environment in the Great Plains would have also added to the ecological stress, forcing rhinos to feed on more nutritious food contents or in a more mesic setting.

In addition to the expansion of C_4 grasslands, environmental changes in the late Miocene, including drying and opening-up of the environment, may have also played a role in the extinction of these rhinos. Large mammals like rhinos are also more vulnerable than smaller mammals in a changing environment, because they usually appear in lesser numbers and so it is harder for them to maintain the genetic diversity needed for survival. The extinction North American rhinos in the Great Plains is likely a result of a combination of these factors.

Large increases in body mass in *Aphelops* occurred from the Clarendonian to Hh2 (Fig. 11) but body mass stabilized in Hh3. A slight decrease in body mass of *Teleoceras* occurred from Hh2 to Hh3, when these rhinos started to decline in abundance. The changes from Hh2 to Hh3 could be an example of body size being affected by lowered primary productivity in the environment. C_4 plants are generally less nutritious as foodstuff for herbivores than C_3 plants, because C_4 vegetation contains less protein and more structural carbohydrates, and is also less digestible (Caswell et al., 1973). Studies have shown that stands of C_4 vegetation support lower herbivore biomass than comparable stands of C_3 vegetation (e.g. Kroh and Beaver, 1978). Expansion of C_4 grasslands in Hh3 would have resulted in lowered net primary productivity in the environment, which may have led to smaller body size in rhinos.

Stable oxygen isotopes in this study did not exhibit significant difference between the sympatric *Aphelops* and *Teleoceras,* as would be expected between terrestrial and semi-aquatic herbivores (Bocherens et al., 1996; Kohn, 1996). A more rigorous test for semi-aquatic lifestyle is to compare $\delta^{18}O_E$ values between a taxon and the contemporaneous medium- to large-bodied herbivore fauna. Based on a model using *Hippopotamus* (Clementz et al., 2008), $\delta^{18}O_E$ values are expected to be significantly lower in "hippo ecomorphs" and plot on the "hippo line." Data from Kita (2011) show that *Teleoceras* $\delta^{18}O_E$ values in two Clarendonian (Pratt Slide and North Shore) and one Hemphillian (Cambridge) locality in Nebraska are not significantly different from those of *Aphelops,* nor do they plot on the hippo line expected for semi-aquatic hippo ecomorphs (Fig. 16).

An alternative hypothesis to explain the evolution of the short-limbed body form of *Teleoceras* was put forth by Matthew (1932), who suggested that the body form was adapted to comparatively smooth, uniform grassy plains, while the longer-limbed, more cursorial *Aphelops* was adapted to open, brushy country with a more irregular topography. This hypothesis has not been adequately tested (Mihlbachler, 2005).

A strong latitudinal oxygen gradient is present in the Great Plains today, following the present-day temperature gradient. The difference between surface water $\delta^{18}O$ values in northwestern Texas and northern Nebraska is approximately 8‰ (Kendall and Coplen, 2001; Dutton et al., 2005). Latitudinal oxygen gradients have been previously documented using stable isotope proxies (e.g. Passey et al., 2002; Fox and Koch, 2003, 2004; Rose et al., 2011). The slope of rhinoceros $\delta^{18}O_E$ against latitude (equation 6) is comparable to those of other proxies (Fig. 17). Fossil horses have higher mean $\delta^{18}O$ values than the other taxa, which is possibly a result of smaller body size or of obtaining water from more evaporated sources. Paleosoil carbonate have the lowest $\delta^{18}O$ values. Slopes are similar for most proxies but the slope is lower in modern bison. The strong correlation between rhino tooth enamel $\delta^{18}O$ values and latitude suggests that rhinoceroses reliably track environmental water $\delta^{18}O$ values and may be a useful proxy for paleoclimatic reconstructions.

6. CONCLUSIONS

The extinction of North American rhinoceroses in the Great Plains at the end of the Hemphillian land mammal age was preceded by a rapid decline in abundance in the Hh3 and Hh4 biochrons (6.9-4.7 Ma). The timing of this decline corresponded closely with the expansion of C_4 grasslands in the Great Plains. Stable carbon isotope compositions of tooth enamel of *Aphelops* and *Teleoceras* indicate that both rhinos remained predominantly C_3 feeders until their extinction, although *Aphelops* may have shifted from browsing to C_3 grazing. Results are consistent with the hypothesis that these rhinoceroses were not able to adapt to the spread of C_4 grasslands and the climate changes associated with it.

Significant body size increase possibly in response to cooling climate was found in both *Aphelops* and *Teleoceras* in the late Miocene, although the increase was much greater in *Aphelops* than *Teleoceras*. Along with a marked decline in abundance in the late Hemphillian, body size stopped increasing in *Aphelops*, which may have been a response to lowered primary productivity with the spread of C_4 grasslands.

Oxygen isotopes in *Aphelops* and *Teleoceras* tooth enamel track a latitudinal oxygen gradient, probably reflecting a meteoric water/temperature gradient. Fossil rhinoceroses are a potentially useful paleoclimate proxy.

REFERENCES

Ashton, K., M. Tracy, and A. Queiroz. 2000. Is Bergmann’s Rule valid for mammals? The American Naturalist 156: 390–415.

Balasse, M., A. B. Smith, S. H. Ambrose, and S. R. Leigh. 2003. Determining sheep birth seasonality by analysis of tooth enamel oxygen isotope ratios: the Late Stone Age site of Kasteelberg (South Africa). Journal of Archaeological Sciences 30: 205–215.

Bales, G. S. 1995. A multivariate morphometric study of living and fossil rhinoceros skulls. Ph.D. Dissertation. University of Southern California, Los Angeles, CA, 416p.

Barry, J.C. 1995. Faunal turnover and diversity in the terrestrial Neogene of Pakistan. Pp. 115-134 in E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Buckle (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. Scientific American 225: 86–93.

Bell, C. J., E. L. Lundelius Jr., A. D. Barnosky, R. W. Graham, E. H. Lindsay, D. R. Ruez Jr., H. A. Semken Jr., S. D. Webb, and R. J. Zakrzewski. 2004. The Blancan, Irvingtonian and Rancholabrean Land Mammal Ages. Pp. 232–314 in M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York.

Blackburn, T., K. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and Distributions 5: 165–174.

Bocherens, H., P. L. Koch, A. Mariotti, D. Geraads, and J. J. Jaeger. 1996. Isotopic biogeochemistry (^{13}C, ^{18}O) of mammalian enamel from African Pleistocene hominid sites. Palaios 11: 306–318.

Bryant, J. D. and P. N. Froelich. 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochimica et Cosmochimica Acta 59: 4523–4537.

Calder, W. A. 1984. Size, Function and Life History. Harvard University Press, Cambridge.

Carrasco, M. A., B. P. Kraatz, E. B. Davis, and A. D. Barnosky, 2005. Miocene Mammal Mapping Project (MIOMAP). University of California Museum of Paleontology, http://www.ucmp.berkeley.edu/miomap/.

Caswell, H., F. Reed, S. N. Stephenson, and P. A. Werner. 1973. Photosynthetic pathways and selective herbivory: a hypothesis. American Naturalist 107: 465–480.

Cerling, T. E. and J. R. Ehleringer. 2000. Welcome to the C_4 world. Pp. 273–286 in R. A. Gastaldo, and W. A. DiMichele (Eds.), Phanerozoic Terrestrial Ecosystems. Yale University Press, New Haven.

Cerling, T. and J. Harris. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120: 347–363.

Cerling, T. E., Y. Wang, and J. Quade. 1993. Expansion of C_4 ecosystems as an indicator of global ecological change in the late Miocene. Nature 361:344–345.

Cerling, T. E., J. M. Harris, B. J. MacFadden, M. G. Leakey, J. Quade, V. Eisenmann, and J. R. Ehleringer. 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389:153–158.

Cerling, T. E., J. R. Ehleringer, and J. M. Harris. 1998. Carbon dioxide starvation, the development of C_4 ecosystems, and mammalian evolution. Philosophical Transactions of the Royal Society of London B 353: 159–171.

Clementz, M. T., P. A. Holroyd, and P. L. Koch. 2008. Identifying aquatic habits of herbivorous mammals through stable isotope analysis. Palaios 23: 574–585.

Cope, E. D. 1879. On the extinct American rhinoceroses and their allies. American Naturalist 13: 771a–771j.

Dansgaard, W. 1964. Stable isotopes in precipitation. Tellus 16: 436–468.

Damuth, J. 1990. Problems in estimating body masses of archaic ungulates using dental measurements. Pp. 229–254 in J. Damuth and B. J. MacFadden (Eds.), Body Size in Mammalian Paleobiology. Cambridge University Press, New York.

Damuth, J. and B. J. MacFadden. 1990. Introduction: body size and its estimations. Pp. 1–10 in J. Damuth, J and B. J. MacFadden (Eds.), Body Size in Mammalian Paleobiology. Cambridge University Press, New York.

Demment, M. W. and P. J. Van Soest. 1985. A nutritional explanation for body size patterns of ruminant and nonruminant herbivores. American Naturalist 125: 641–672.

Diefendorf, A. F., K. E. Mueller, S. L. Wing, P. L. Koch, and K. H. Freeman. 2010. Global patterns in leaf ^{13}C discrimination and implications for studies of past and future climate. Proceedings of the National Academy of Sciences 107: 5738–5743.

Diffendal, R. F. and M. R. Voorhies. 1994. Geologic framework of the Niobrara River Drainage Basin and adjacent areas in South Dakota generally east of the 100th Meridian West Longitude and west of the Missouri River. Nebraska Geological Survey Report of Investigations 9:1–13.

Dutton, A., B. Wilkinson, J. Welker, G. Bowen, and K. Lohmann. 2005 Spatial distribution and seasonal variation in $^{18}O/^{16}O$ of modern precipitation and river water across the conterminous USA. Hydrological Processes19: 4121–4146.

Edwards, E. J., C. P. Osborne, C. A. E. Strömberg, S. A. Smith, and C_4 Grasses Consortium. 2010. The origins of C_4 grasslands: integrating evolutionary and ecosystem science. Science 328:587–591.

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

Ehleringer, J. R., R. F. Sage, L. B. Flanagan, and R. W. Pearcy. 1991. Climate change and the evolution of C_4 photosynthesis. Trends in Ecology and Evolution 6: 95–99.

Eronen, J. T., M. M. Ataabadia, A. Micheelsb, A. Karme, R. L. Bernor, and M. Fortelius. 2009. Distribution history and climatic controls of the Late Miocene Pikermian chronofauna. Proceedings of the National Academy of Sciences 106: 11867–11871.

Farlow, J. O., J. A. Sunderman, J. J. Havens, A. L. Swinehart, J. A. Holman, R. L. Richards, N. G. Miller, R. A. Martin, R. M. Hunt Jr., G. G. Storrs, B. B. Curry, R. H. Fluegeman, M. R. Dawson, and M. E. T. Flint. 2001. The Pipe Creek Sinkhole Biota, a diverse late Tertiary continental fossil assemblage from Grant County, Indiana. American Midland Naturalist 145:367–378.

Feranec, R. S. 2003. Stable isotopes, hypsodonty, and the paleodiet of Hemiauchenia (Mammalia: Camelidae): a morphological specialization creating ecological generalization. Paleobiology 29: 230–242.

Feranec, R. S. 2007. Stable carbon isotope values reveal evidence of resource partitioning among ungulates from modern C_3-dominated ecosystems in North America. Palaeogeography, Palaeoclimatology, Palaeoecology 252: 575–585.

Feranec, R. S. and B. J. MacFadden. 2006. Isotopic discrimination of resource partitioning among ungulates in C_3-dominated communities from the Miocene of Florida and California. Paleobiology 32: 191–205.

Fox, D. L. and P. L. Koch. 2003. Tertiary history of C_4 biomass in the Great Plains, USA. Geology 31:809–812.

Fox, D.L. and P. L. Koch. 2004. Carbon and oxygen isotopic variability in Neogene paleosol carbonates: constraints on the evolution of the C_4-grasslands of the Great Plains, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 207: 305–329.

Fricke, H. C. and J. R. O'Neil. 1999. The correlation between $^{18}O/^{16}O$ ratios of meteoric water and surface temperature: its use in investigating terrestrial climate change over geologic time. Earth and Planetary Science Letters 170: 181–196.

Gardner, J., A. Peters, M. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming? Trends in Ecology and Evolution 26: 285–291.

Gat, J. R. 1996. Oxygen and hydrogen isotopes in the hydrologic cycle. Annual Review of Earth and Planetary Sciences 24: 225–262.

Gregory, J. T. 1942. Pliocene vertebrates from Big Spring Canyon South Dakota. University of California Publications in Geological Sciences 26: 307-446.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. American Zoologist 14: 205–220.

Gustafson, E. P. 2012. New records of rhinoceroses from the Ringold Formation of central Washington and the Hemphillian-Blancan boundary. Journal of Vertebrate Paleontology 32 (3): 727–731.

Heaton, T. H. E. 1999. Spatial, species, and temporal variations in the $^{13}C/^{12}C$ ratios of C_3 plants: implications for paleodiet studies. Journal of Archaeological Science 26, 637–649.

Helliker, B. R. and J. R. Ehleringer. 2002. Differential ^{18}O enrichment of leaf cellulose in C_3 versus C_4 grasses. Functional Plant Biology 29: 435–442.

Hoppe, A. K. 2006. Correlation between the oxygen isotope ratio of North American bison teeth and local waters: Implications for paleoclimatic reconstructions. Earth and Planetary Science Letters 244: 408–417.

Howell, A. B. 1965. Speed in Animals: Their Specialization for Running and Leaping. Hafner, London.

Iacumin, P. and A. Longinelli. 2002. Relationship between $\delta^{18}O$ values for skeletal apatite from reindeer and foxes and yearly mean $\delta^{18}O$ values of environmental water. Earth and Planetary Science Letters 201: 213–219.

Janis, C. M. 1990. Correlation of cranial and dental variables with body size ungulates and macropodoids. Pp. 255–300 in J. Damuth and B. J. MacFadden (Eds.), Body Size in Mammalian Paleobiology. Cambridge University Press, New York.

Janis, C. M., J. Damuth, and J. M. Theodor. 2000. Miocene ungulates and terrestrial primary productivity: Where have all the browsers gone? Proceedings of the National Academy of Science 97: 7899.

Janis, C. M., J. Damuth, and J. M. Theodor. 2002. The origins and evolution of the North American grassland biome: the story from the hoofed mammals. Palaeogeography, Palaeoclimatology, Palaeoecology 177: 183–198.

Janis, C. M., J. Damuth, and J. M. Theodor. 2004. The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 371–398.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48: 215–266.

Kendall, C. and T. B. Coplen. 2001. Distribution of oxygen-18 and deuterium in river waters across the United States. Hydrological Processes 15: 1363–1393.

Kita, Z. A. 1999. New stable isotope record of paleoecological change in the late Neogene of the western Great Plains from enamel in large mammals. M.S. Thesis. University of Nebraska, Lincoln, Nebraska, 87 p.

Kita, Z. A., R. Secord, and G. S. Boardman. 2014. A new stable isotope record of Neogene paleoenvironments and mammalian paleoecologies in the western Great Plains during the expansion of C4 grasslands. Palaeogeography, Palaeoclimatology, Palaeoecology 399:160–172.

Koch, P. L. 1998. Isotopic reconstruction of past continental environments. Annual Review of Earth and Planetary Sciences 26: 573–613.

Koch, P. L., N. Tuross, and M. L. Fogel. 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. Journal of Archaeological Science 24: 417–429.

Koch, P. L., K. A. Hoppe, and S. D. Webb. 1998, The isotopic ecology of late Pleistocene mammals in North America part 1. Florida. Chemical Geology152: 119–138.

Koch, P. L., W. C. Clyde, R. P. Hepple, M. L. Fogel, S. L. Wing, and J. C Zachos. 2003. Carbon and oxygen isotope records from paleosols spanning the Paleocene–Eocene boundary, Bighorn Basin, Wyoming. Pp. 49–64 in S. L Wing, P. D. Gingerich, B. Schmitz, and E. Thomas (Eds.), Causes and Consequences of Globally Warm Climates in the Early Paleogene Volume 369. Boulder, Geological Society of America Special Paper, 369.

Kohn, M. J. 1996. Predicting animal δ^{18}O: accounting for diet and physiological adaptation. Geochimica et Cosmochimica Acta 60: 4811–4829.

Kohn, M. J. 2010. Carbon isotope compositions of terrestrial C_3 plants as indicators of (paleo)ecology and (paleo)climate. Proceedings of the National Academy of Science 107: 19691–19695.

Kohn, M. J. and J. M. Welker. 2005. On the temperature correlation of δ^{18}O in modern precipitation. Earth and Planetary Science Letters 231: 87–96.

Kohn, M. J., M. J. Schoeninger, and J. W. Valley. 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. Geochimica et Cosmochimica Acta

60: 3889–3896.

Kohn, M. J., M. J. Schoeninger, and J. W. Valley. 1998. Variability in oxygen isotope compositions of herbivore teeth: reflections of seasonality or developmental physiology? Chemical Geology 152: 97–112.

Kroh, G., and D. L. Beaver. 1978. Insect responses to mixture and monoculture patches of Michigan old-field annual herbs. Oecologia 31: 269–275.

Lambert, W. D. 1994. The fauna and paleoecology of the late Miocene Moss Acres Racetrack Site, Marion County, Florida. Ph.D. Dissertation. University of Florida, Gainesville, 356 p.

Land, L. S., E. L. Lundelius Jr., and S. Valastro Jr. 1980. Isotopic ecology of deer bones. Palaeogeography, Palaeoclimatology, Palaeoecology 32: 143–151.

Latorre, C., J. Quade, and W. C. McIntosh. 1997. The expansion of C_4 grasses and global change in the late Miocene: stable isotope evidence from the Americas. Earth and Planetary Science Letters 146: 83–96.

Leakey, M. G., C. S. Feibel, R. L. Bernor, J. M. Harris, T. E. Cerling, K. M. Stewart, G. W. Storrs, A. Walker, L. Werdelin, and A. J. Winkler. 1996. Lothagam: a record of faunal change in the Late Miocene of East Africa. Journal of Vertebrate Paleontology 16: 556–570.

Lee-Thorp, J. A. and N. J. van der Merwe. 1987. Carbon isotope analysis of fossil bone apatite. South African Journal of Science 83: 712–715.

Levin, N. E., T. E. Cerling, B. H. Passey, J. M. Harris, J. R. Ehleringer. 2006. A stable isotope aridity index for terrestrial environments. Proceedings of the National Academy of Science 103: 11201–11205.

Lindsay, E. H. 2003. Chronostratigraphy, biochronology, datum events, land mammal ages, stage of evolution, and appearance event ordination. Bulletin of American Museum of Natural History 279: 212–230.

Longinelli, A. 1984. Oxygen isotopes in mammal bone phosphate: A new tool for paleohydrological and paleoclimatological research? Geochimica et Cosmochimica Acta 48: 385–390.

Luz, B. and Y. Kolodny. 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV. Mammal teeth and bones. Earth and Planetary Science Letters 75: 29–36.

MacFadden, B. J. 1992. Fossil horses: systematics, paleobiology, and evolution of the Family Equidae. Cambridge University Press, New York.

MacFadden, B. J. 1998. Tale of two rhinos: isotopic ecology, paleodiet, and niche differentiation of *Aphelops* and *Teloceras* from the Florida Neogene. Paleobiology 24: 274–286.

MacFadden, B. J., and T. E. Cerling. 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10 million-year sequence from the Neogene of Florida. Journal of Vertebrate Paleontology 16: 103–115.

MacFadden, B. J., T. E. Cerling, J. M Harris, and J. Prado. 1999. Ancient latitudinal gradients of C_3/C_4 grasses interpreted from stable isotopes of New World Pleistocene horse (*Equus*) teeth. Global Ecology and Biogeography 8: 137–149.

Madden, C. T. and W. W. Dahlquest. 1990. The last rhinoceros in North America. Journal of Vertebrate Paleontology 10: 266–267.

Martin, R. A., H. T. Goodwin, and J. O. Farlow. 2002. Late Neogene (late Hemphillian) rodents from the Pipe Creek sinkhole, Grant County, Indiana. Journal of Vertebrate Paleontology 22: 137–151.

Matthew, W. D. 1932. A review of the rhinoceroses with a description of *Aphelops* material from the Pliocene of Texas. University of California Publications, Bulletin of the Department of Geological Sciences 20: 411–480.

Mayr, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, MA.

Mead, A. J. 1999. Aspects of the systematics and paleoecologies of the middle to late Miocene North American rhinoceroses *Peraceras, Teleoceras,* and *Aphelops*. Ph.D. Dissertation. University of Nebraska, Lincoln, Nebraska, 308 p.

Mead, A.J. 2000. Sexual dimorphism and paleoecology in *Teleoceras*, a North American rhinoceros. Paleobiology 26: 689–706.

Mendoza, M. and P. Palmqvist. 2008. Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? Journal of Zoology 274: 134–142.

Mihlbachler, M. C. 2003. Demography of late Miocene rhinoceroses (*Teleoceras proterum* and *Aphelops malacorhinus*) from Florida: linking mortality and sociality in fossil assemblages. Paleobiology 29: 412–428.

Mihlbachler, M. C. 2005. Linking sexual dimorphism and sociality in rhinoceroses: insights from *Teleoceras proterum and Aphelops malacorhinus* from the late Miocene of Florida. Pp. 495–520 in R. C. Hulbert Jr., G. S. Morgan, and J. A. Baskin (Eds.), Cenozoic Vertebrates of the Americas: Papers to Honor S. David Webb. Bulletin of the Florida Museum of Natural History 45.

McNab, B. 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. Oecologia 164: 13–23.

Müller, D. W. H., D. Codron, C. Meloro, A. Munn, A. Schwarm, J. Hummel, and M. Clauss. 2013. Assessing the Bell-Jarman principle: scale of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. Comparative Biochemistry and Physiology, Part A 164 (1):129-140.

O'Leary, M. H. 1988. Carbon isotopes in photosynthesis. Bioscience 38: 328–336.

O'Leary, M. H., S. Madhavan, and P. Paneth. 1992. Physical and chemical basis of carbon isotope fractionation in plants. Plant, Cell & Environment 15: 1099–1104.

Osborn, H. F. 1898a. A complete skeleton of *Teleoceras fossiger*: Notes upon the growth and sexual characters of this species. Bulletin of the American Museum of Natural History 10: 51–59.

Osborn, H. F. 1898b. A complete skeleton of *Teleoceras* the true rhinoceros from the Upper Miocene of Kansas. Science 7: 554–557.

Osborn, H. F. 1904. New Miocene rhinoceroses: with revisions of known species. Bulletin of the American Museum of Natural History 20: 307–326.

Owen-Smith, N. 1982. Factors influencing the consumption of plant products by large herbivores. Pp. 359–404 in B. J. Huntley and B. H. Walker BH (Edsx), Ecology of tropical savannas. Springer, Berlin Heidelberg New York.

Paleobiology Database. www.paleobiodb.org. Accessed September 2014–May 2016.

Passey, B. H., T. E. Cerling, M. E. Perkins, M. R. Voorhies, J. M. Harris, and S. T. Tucker. 2002. Environmental change in the Great Plains: an isotopic record from fossil horses. Journal of Geology 110: 123–140.

Passey, B. H., T. F. Robinson, L. K. Ayliffe, T. E. Cerling, M. Sponheimer, M. D. Dearling, B. L. Roeder, and J. R. Ehleringer. 2005. Carbon isotope fractionation between diet, breath CO_2, and bioapatite in different mammals, Journal of Archaeological Science 32: 1459–1470.

Peñuelas, J. and I. Filella. 2001. Responses to a warming world. Science 294: 793–795.

Peters, R. H. 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Prothero, D. R. 1992. Fifty million years of rhinoceros evolution. Pp. 82-91 in O. A. Ryder (Ed.), Rhinoceros biology and conservation. Zoological Society, San Diego.

Prothero, D.R. 1993. Ungulate phylogeny: molecular vs. morphological evidence. Pp. 173–181 in F. S. Szalay, M. J. Novacek, and M. C. McKenna (Eds.), Mammal Phylogeny. Vol. II: Placentals. Springer-Verlag, New York.

Prothero, D. R. 1998. Rhinocerotidae. Pp. 595-605 in C. M. Janis, K. M. Scott, and L. L. Jacobs (Eds.), Evolution of Tertiary mammals of North America. Cambridge University Press, Cambridge.

Prothero, D. R. 2005. The Evolution of North American Rhinoceroses. Cambridge University Press, New York.

Prothero, D. R. and E. M. Manning. 1987. Miocene rhinoceroses from the Texas Gulf Coastal Plain. Journal of Paleontology 61: 388–423.

Prothero, D. R., C. Guérin, and E. Manning. 1989. The history of the Rhinoceratoidea. Pp. 320-340 in D. R. Prothero and R. M. Schoch (Eds.), The evolution of perissodactyls. Oxford University Press, New York

Rozanski, K., L. Araguás-Araguás, and R. Gonfiantini. 1992. Relation between long-term trends of oxygen-18 isotope composition of precipitation and climate. Science 258: 981–985.

Rodríguez, M., M. Olalla-Tárraga, and B. Hawkins. 2008. Bergmann's rule and the geography of mammal body size in the western hemisphere. Global Ecology and Biogeography 17: 274–283.

Rose, P. J., D. L. Fox, J. Marcot, and C. Badgley. 2011. Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. Geology 39: 163–166.

Secord, R., S. L. Wing, and A. Chew. 2008. Stable isotopes in early Eocene mammals as indicators of forest canopy structure and resource partitioning. Paleobiology 34: 282–300.

Secord, R., P. D. Gingerich, K. C. Lohmann, and K. G. MacLeod. 2010. Continental warming preceding the Palaeocene–Eocene thermal maximum. Nature 467: 955–958.

Secord, R., J. I. Bloch, S. G. B. Chester, D. M. Boyer, A. R. Wood, S. L. Wing, M. J. Kraus, F. A. McInerney, and J. Krigbaum. 2012. Evolution of the earliest horses driven by climate change in the Paleocene-Eocene Thermal Maximum. Science 335: 959–962.

Schultz, C. B., T. M. Stout, C. H. Falkenbach, L. G. Tanner, H. J. Cook, and A. L. Lugn. 1961. Field conference on the Tertiary and Pleistocene of western Nebraska. Special Publication of the University of Nebraska State Museum 2:1–55.

Scott, W. B. 1913. A history of land mammals in the western hemisphere. Macmillan, New York.

Sharp, Z. 2007. Principles of Stable Isotope Geochemistry. Pearson Prentice Hall, Upper Saddle River.

Silva, M. and J. A. Downing. 1995. CRC handbook of mammalian body masses. CRC Press, Boca Raton, FL.

Simpson, G. G. 1945. The principles of classification and a classification of the mammals. Bulletin of the American Museum of Natural History 85: 1–350.

Stewart, G. R., M. H. Turnbull, S. Schmidt, and P. D. Erskine. 1995. ^{13}C natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. Australian Journal of Plant Physiology 22: 51–55.

Strömberg, C. A. E. 2006. Evolution of hypsodonty in equids: testing a hypothesis of adaptation. Paleobiology 32:236–258.

Strömberg, C. A. E. and F. A. McInerney. 2011. The Neogene transition from C3 to C4 grasslands in North America: assemblage analysis of fossil phytoliths. Paleobiology 37:50–71.

Tedford, R. H., L. B. Albright III, A. D. Barnosky, I. Ferrusquia-Villafranca, R. M. Hunt, Jr., J. E. Storere, C. C. Swosher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler.2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). Pp. 169–231 in M. O. Woodburne (Ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York.

Teeri, J. A. and L. G. Stowe. 1976. Climatic patterns and the distribution of C_4 grasses in North America. Oecologia 23: 1–12.

Tipple, B. J. and M. Pagani. 2007. The early origins of terrestrial C_4 photosynthesis. Annual Review of Earth and Planetary Sciences 35: 435–461.

Tütken, T. and T. Vennemann. 2009. Stable isotope ecology of Miocene large mammals from Sandelzhausen, southern Germany. Palaeontologische Zeitschrift 83: 207–226.

U.S. Geological Survey. www.usgs.gov. Accessed September 2014–May 2016.

Voorhies, M. R. 1981. Dwarfing the St. Helens eruption: ancient ashfall creates a Pompeii of prehistoric animals. National Geographic 159: 66–75.

Yakir, D. 1992. Variations in the natural abundance of oxygen-18 and deuterium in plant carbohydrates. Plant, Cell & Environment 15: 1005–1020.

Yakir, D., M. J. DeNiro, and J. R. Gat. 1990. Natural deuterium and oxygen-18 enrichment in leaf water of cotton plants grown under wet and dry conditions: evidence for water compartmentation and its dynamics. Plant, Cell & Environment 13: 49–56.

Voorhies, M. R. 1983. Vertebrate paleontology of the proposed Norden Reservoir area, Brown, Cherry, and Keya Paha Counties, Nebraska. Division of Archeological Research, Department of Anthropology, University of Nebraska–Lincoln, Technical Report 82-09.

Voorhies, M. R. 1985. A Miocene rhinoceros herd buried in volcanic ash. Research Reports of the National Geographic Society 19:671-688.

Voorhies, M.R., 1990. Vertebrate Biostratigraphy of the Ogallala Group in Nebraska. Pp. 115-155 in T. C. Gustavson (Ed.), Geologic Framework and Regional Hydrology: Upper Cenozoic Blackwater Draw and Ogallala Formations, Great Plains. University of Texas Press, Austin.

Voorhies, M. R. and S. G. Stover. 1978. An articulated fossil skeleton of a pregnant rhinoceros, *Teleoceras major* Hatcher. Proceedings of the Nebraska Academy of Sciences 88: 47–48.

Voorhies, M. R. and J. R. Thomasson. 1979. Fossil grass anthoecia within Miocene rhinoceros skeletons: diet in an extinct species. Science 206: 331–333.

Wall, W. P. and K. L. Heinbaugh. 1999. Locomotor adaptations in *Metamynodon planifrons* compared to other amynodontids (Perissodactyla, Rhinocerotoidea). National Parks Paleontological Research 4: 8–17.

Wang, Y., T. E. Cerling, and B. J. MacFadden. 1994. Fossil horses and carbon isotopes: new evidence for Cenozoic dietary, habitat, and ecosystem changes in North America. Palaeogeography, Palaeoclimatology, Palaeoecology 107: 269–279.

Webb, S. D. 1983. The rise and fall of the late Miocene ungulate fauna in North America. Pp. 267-306 in M. H. Nitecki. (Ed.), Co-evolution. University of Chicago Press, Chicago.

Webb, S. D. and N. D. Opdyke. 1995. Global climatic influence on Cenozoic land mammal faunas. Pp. 184-208 in National Research Council (Ed.), Global Climatic

Influence on Cenozoic Land Mammal Faunas. National Academy Press, Washington, D.C.

Wood, H. E., R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, Jr., and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. Geological Society of America Bulletin 52:1-48.

Woodburne, M. O. 2004. Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686–693.

Zachos, J. C., G. R. Dickens, and R. E. Zeebe. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451: 279–283.

Zanazzi, A. and M. J. Kohn. 2008. Ecology and physiology of White River mammals based on stable isotope ratios of teeth. Palaeogeography, Palaeoclimatology, Palaeoecology 257: 22–37.

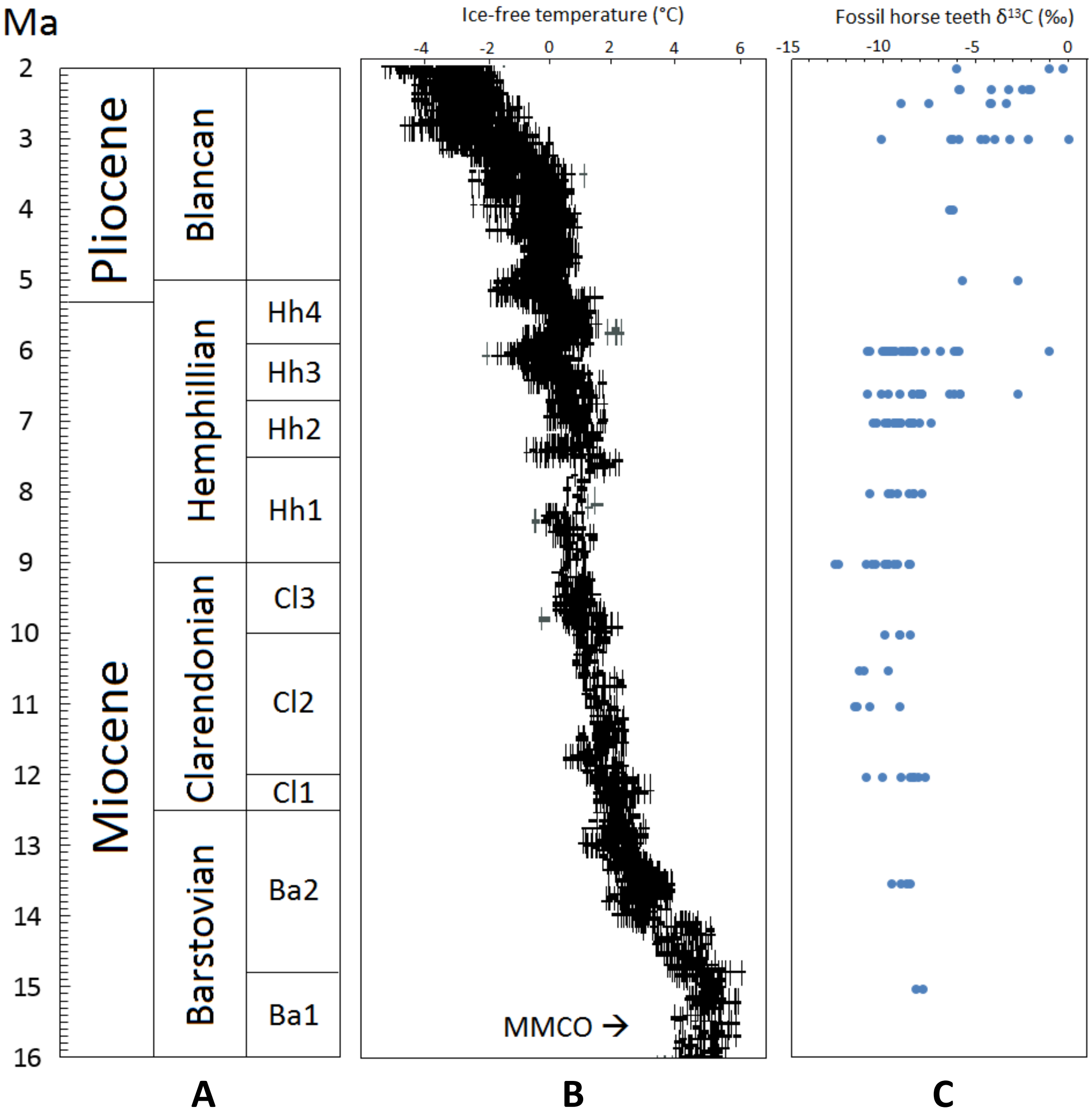

Figure 1. Charts showing correlation of mammalian biochrons, marine benthic temperature record, and carbon isotopes in horse teeth from the Great Plains. (A) Geochronologic chart showing from left to right: Epochs, North American land-mammal ages, and North American mammalian biochrons. After Tedford et al., 2004. (B) Marine benthic temperature derived from oxygen isotopes in foraminifera (Zachos et al., 2008). Note progressive cooling after the Mid-Miocene Climatic Optimum (MMCO). (C) Carbon isotope values from horse tooth enamel from the Great Plains (Passey et al., 2002). Note the increase in values in the late Miocene and Pliocene, indicating increased C_4 consumption.

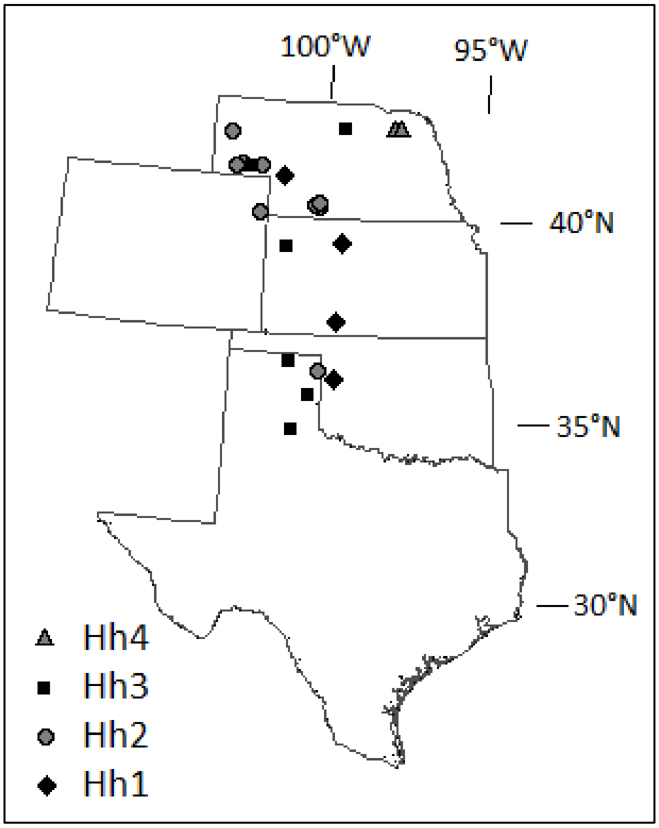

Figure 2. Age and distribution of fossil localities sampled for stable isotope analysis.

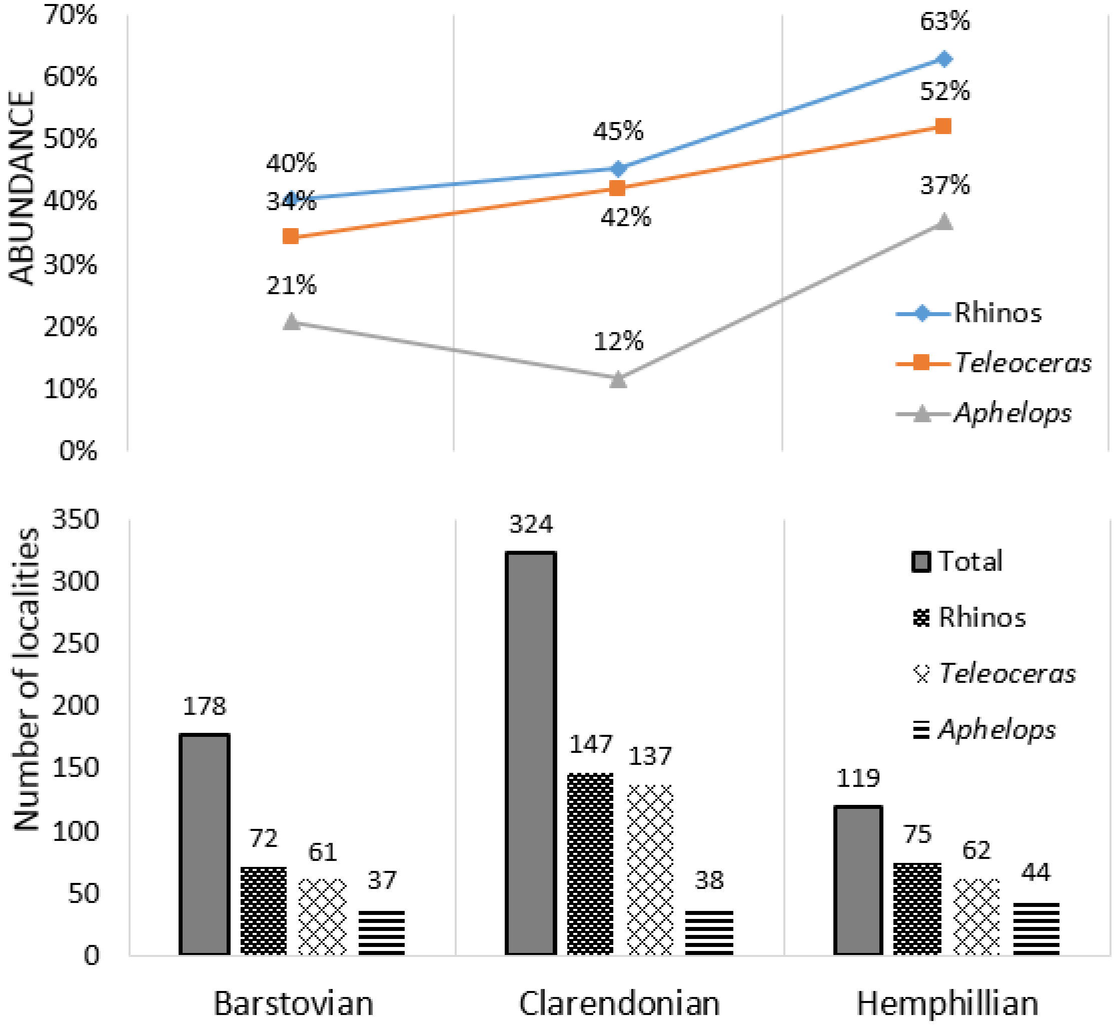

Figure 3. Numbers of localities and relative abundance of *Aphelops* and *Teleoceras* in the Barstovian, Clarendonian, and Hemphillian land mammal ages. Abundances are calculated percentages of localities that contain fossil rhinoceroses.

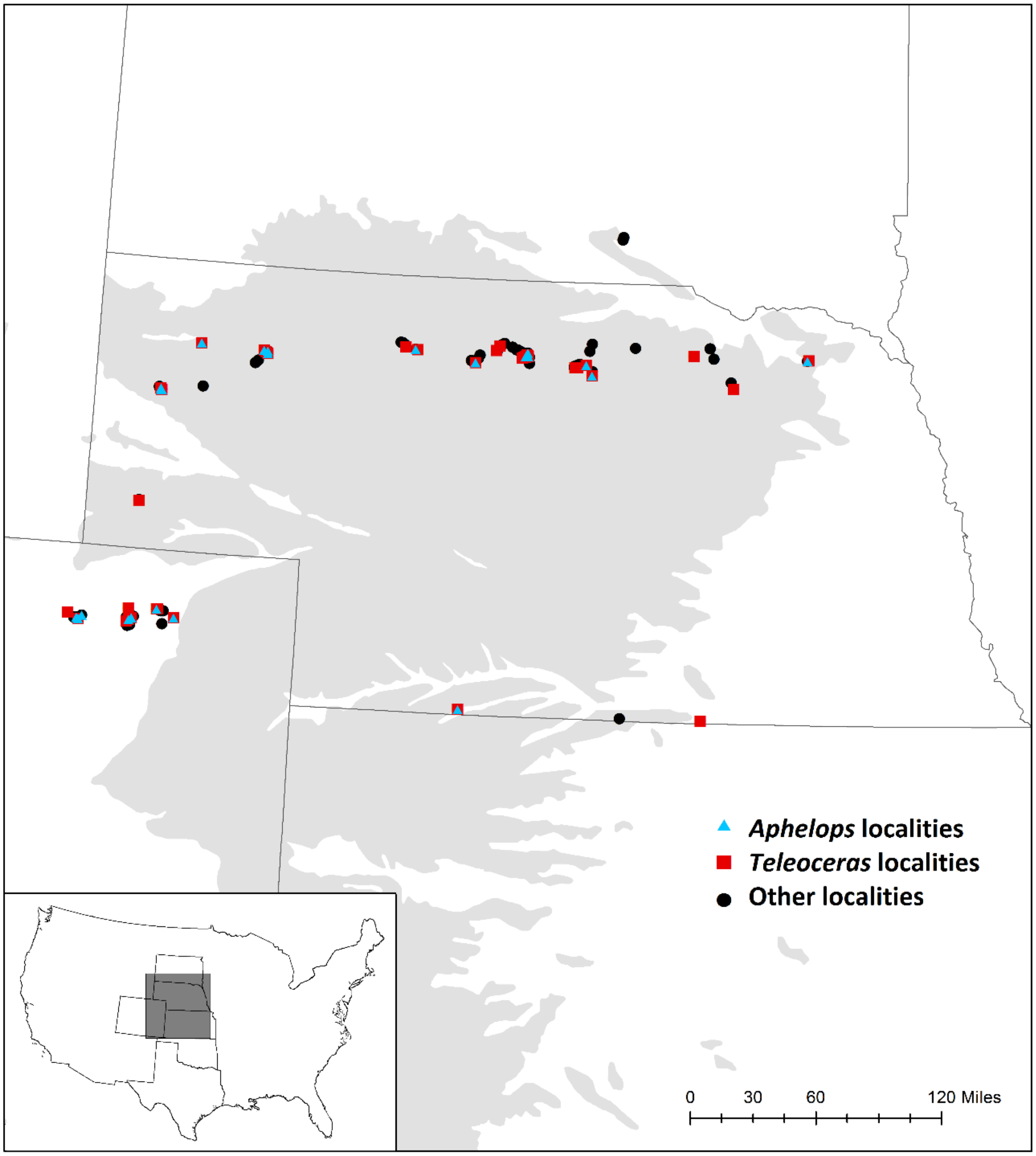

Figure 4. Distribution of Barstovian localities. Gray area represents Neogene rock formations, primarily the Ogallala Group.

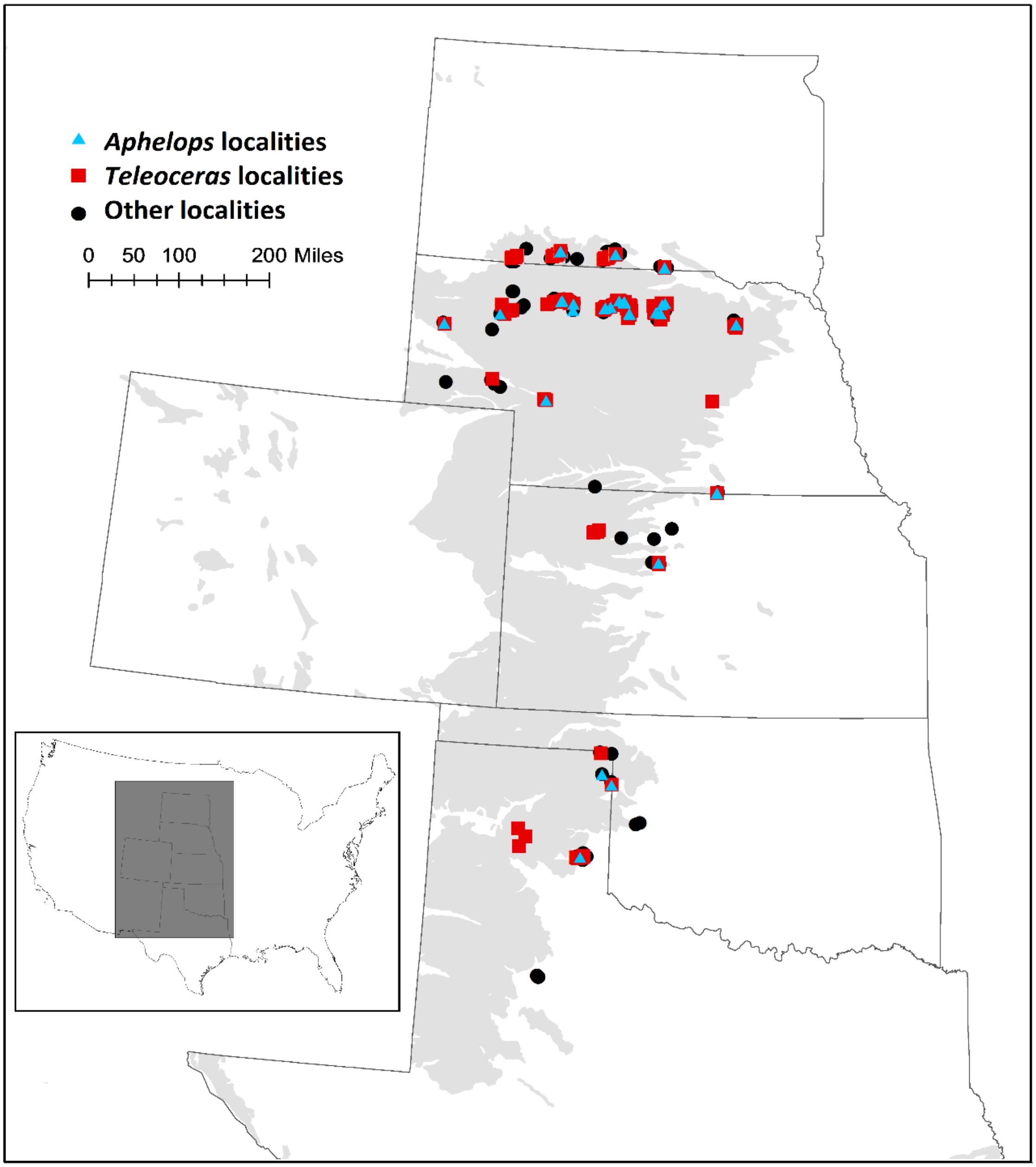

Figure 5. Distribution of Clarendonian localities. Gray area represents Neogene rock formations, primarily the Ogallala Group.

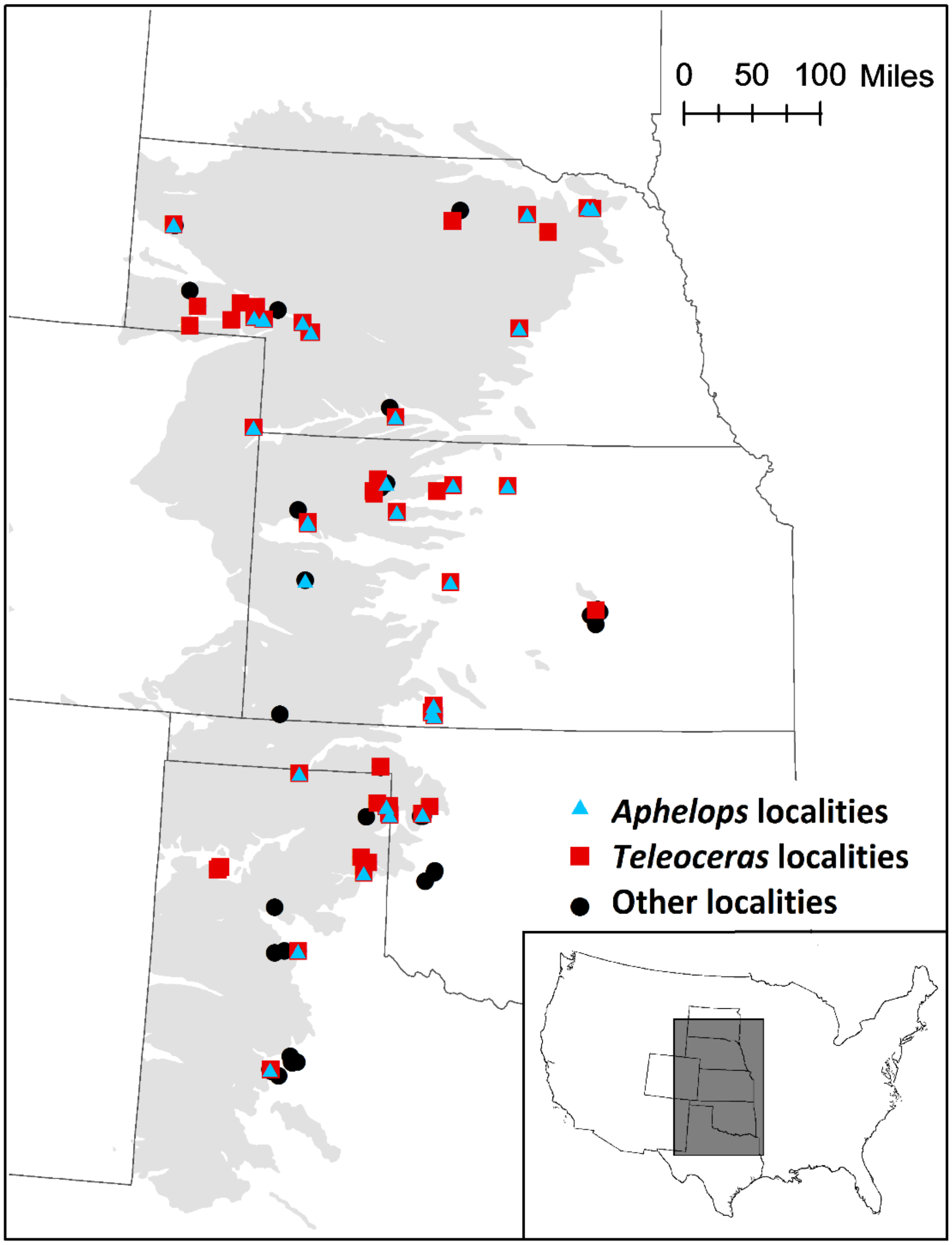

Figure 6. Distribution of Hemphillian localities. Gray area represents Neogene rock formations, primarily the Ogallala Group.

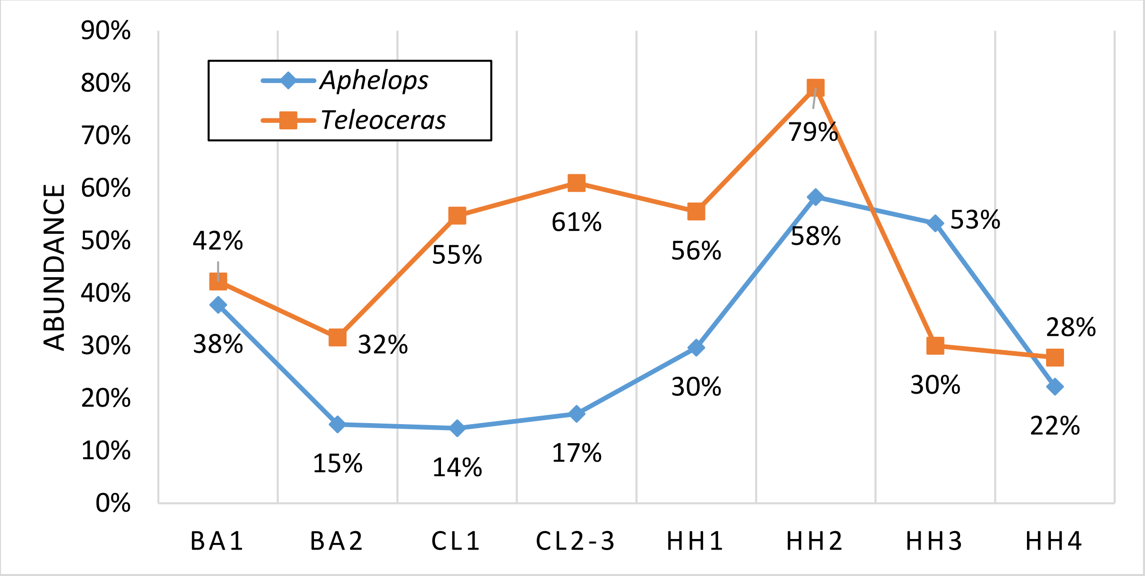

Figure 7. Relative abundance of *Aphelops* and *Teleoceras* through time at the biochron scale.

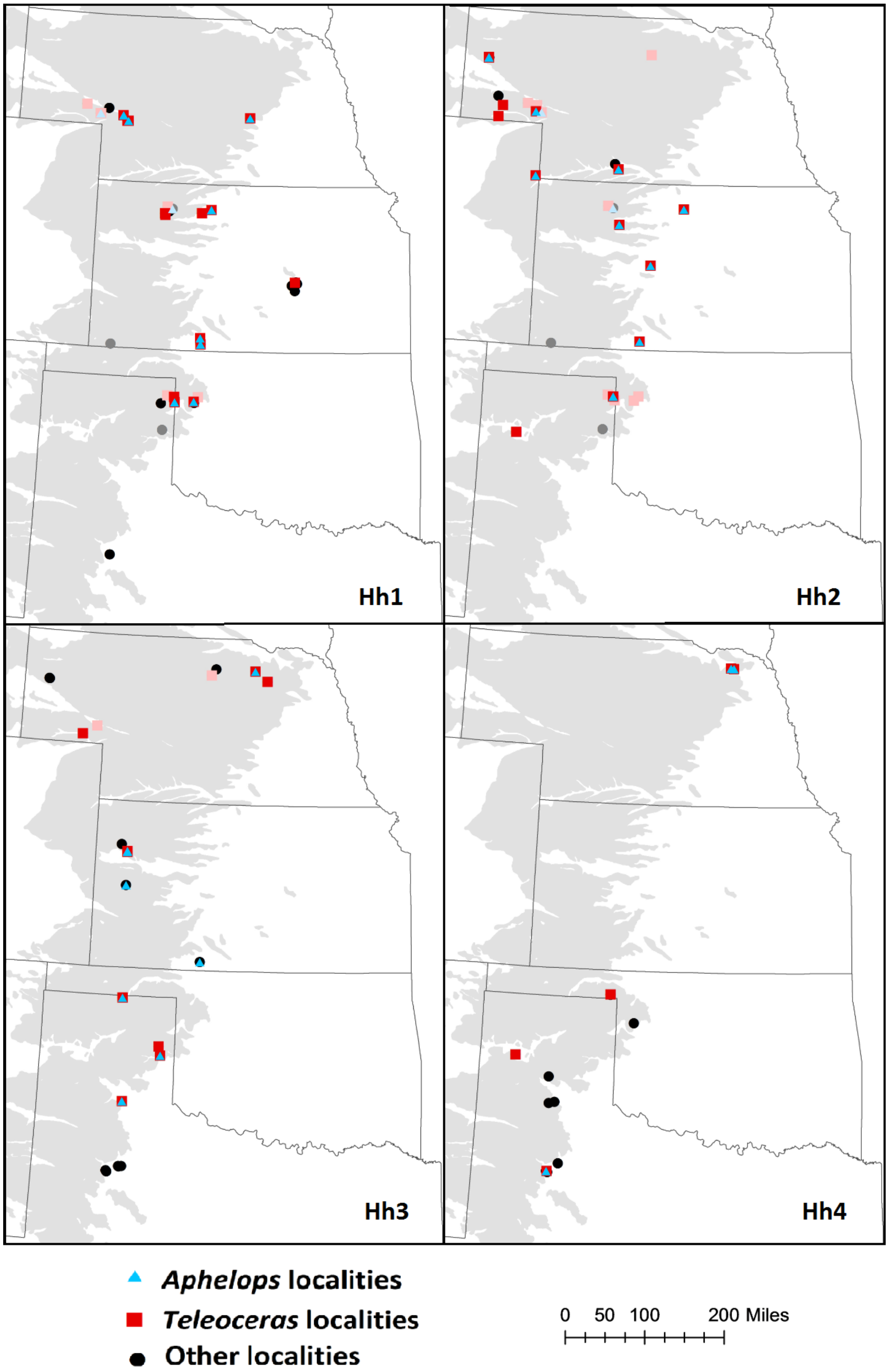

Figure 8. Distribution of Hemphillian localities by biochron. Gray area represents Neogene rock formations, primarily the Ogallala Group. Light colored symbols represent localities with uncertain age.

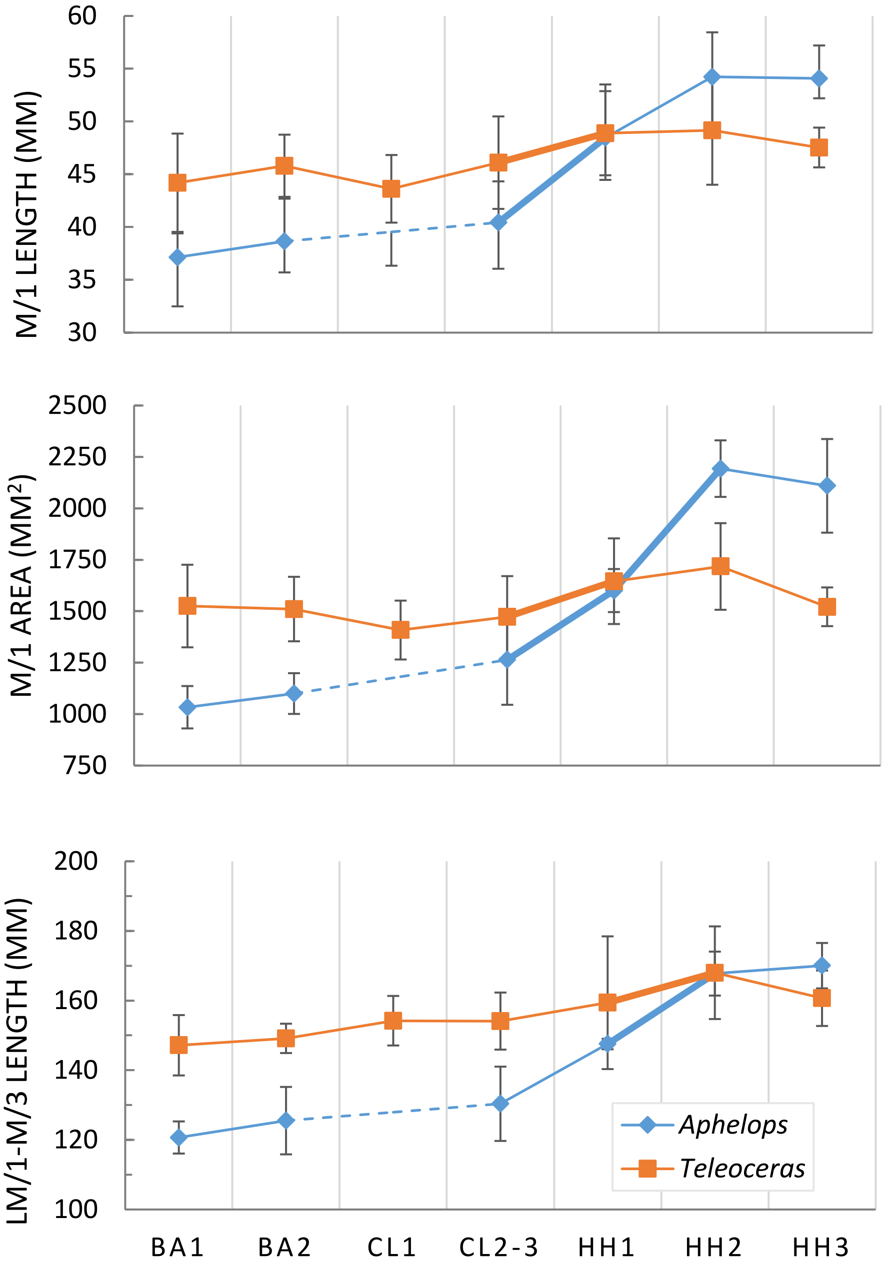

Figure 9. Comparison of the three body mass proxies between *Aphelops* and *Teleoceras*. Error bar denotes one standard deviation. Thick lines indicate significant changes (p<0.05, t-test).

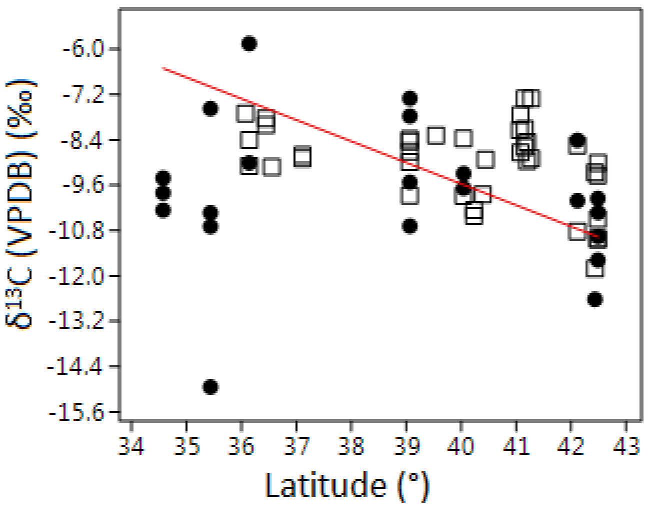

Figure 10. Correlation between latitude and $\delta^{13}C$ values of rhinoceros tooth enamel. Filled circle = *Aphelops*. Open square = *Teleoceras*. Reduced major axis regression yields the equation: $\delta^{13}C_E = -0.56 (\pm 0.07) * \text{Latitude} + 12.99(\pm 8.30)$ ($r^2 = 0.02$, p=0.26). No significant correlation is found.

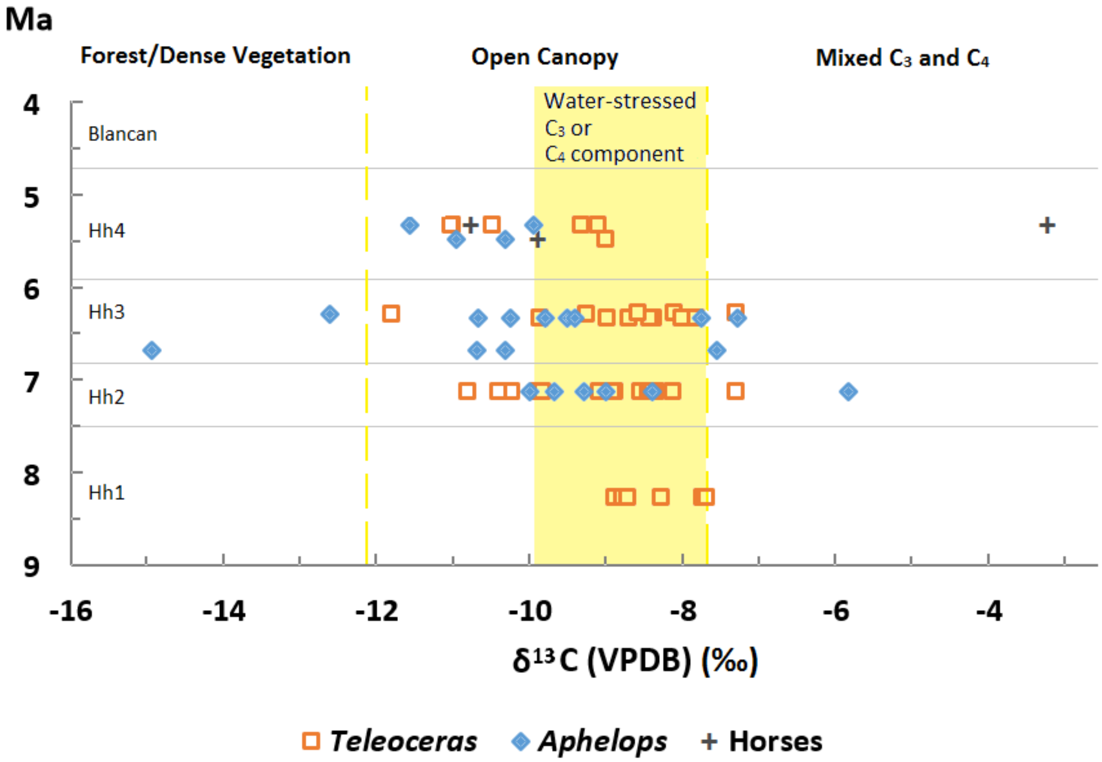

Figure 11. Individual $\delta^{13}C_E$ values for rhinos and horses and boundaries between vegetation types.

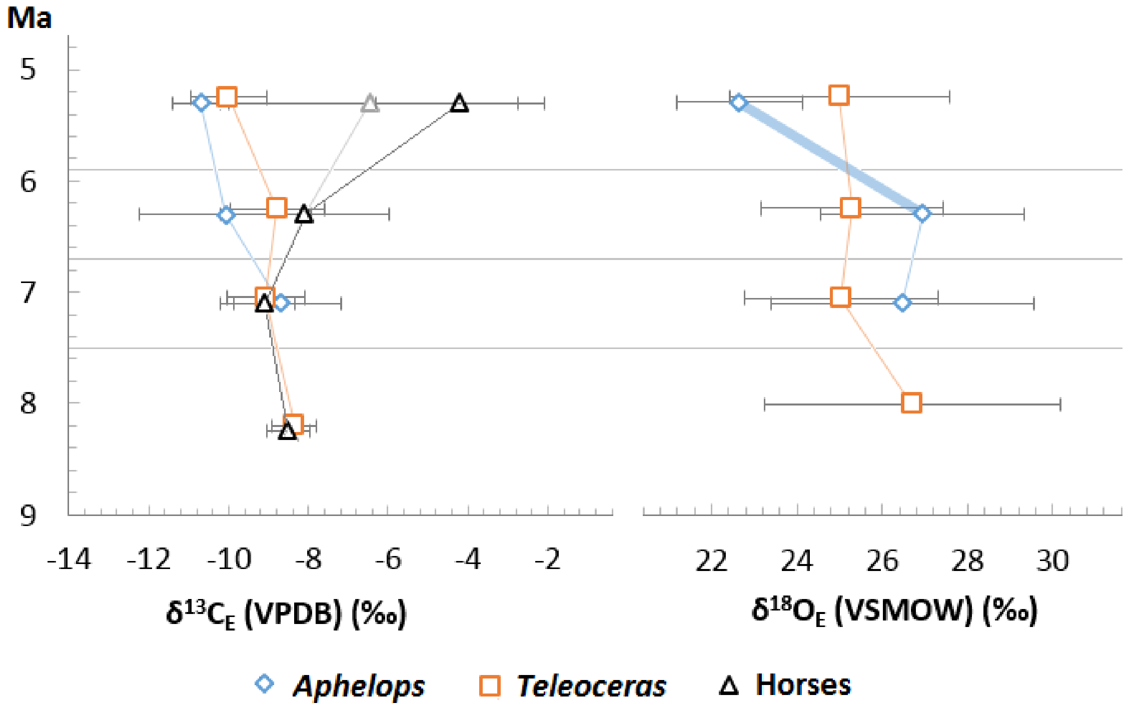

Figure 12. Mean $\delta^{13}C_E$ and $\delta^{18}O_E$ values at each biochron. Thick line represents significant ($p<0.05$, *t*-test) change. Fossil horse data are from Passey et al. (2002). Mean $\delta^{13}C_E$ values of horses in Hh4 are calculated using only data from Passey et al. (black) and using data from both Passey et al. and this study (gray).

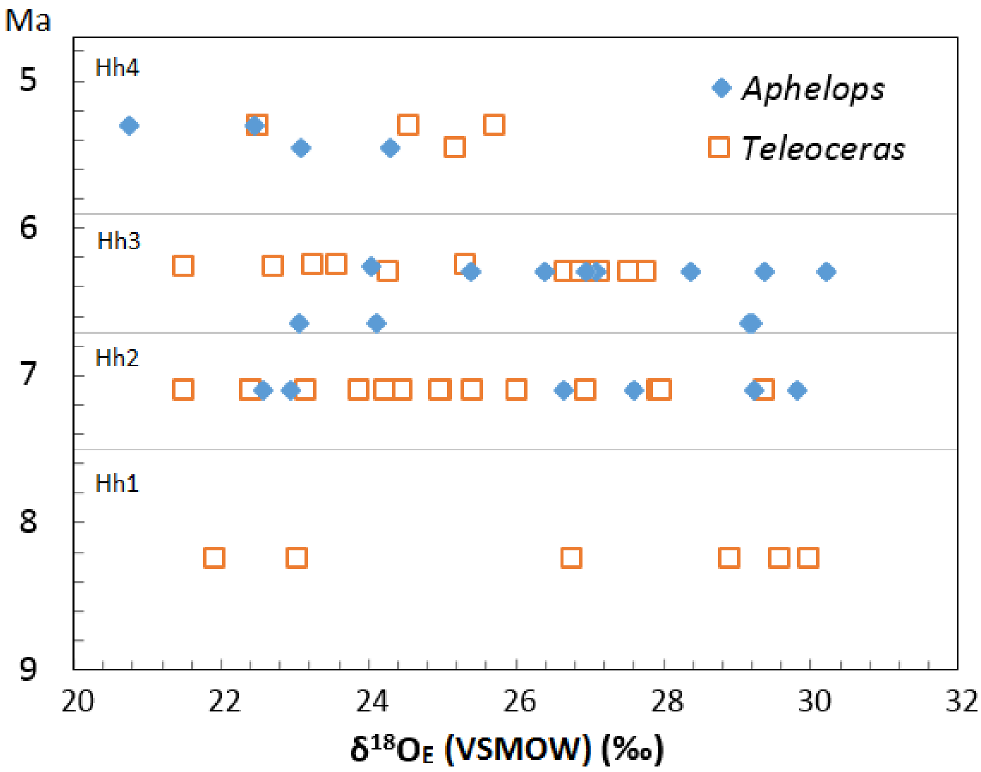

Figure 13. Individual $\delta^{18}O_E$ values for rhinos through the Hemphillian.

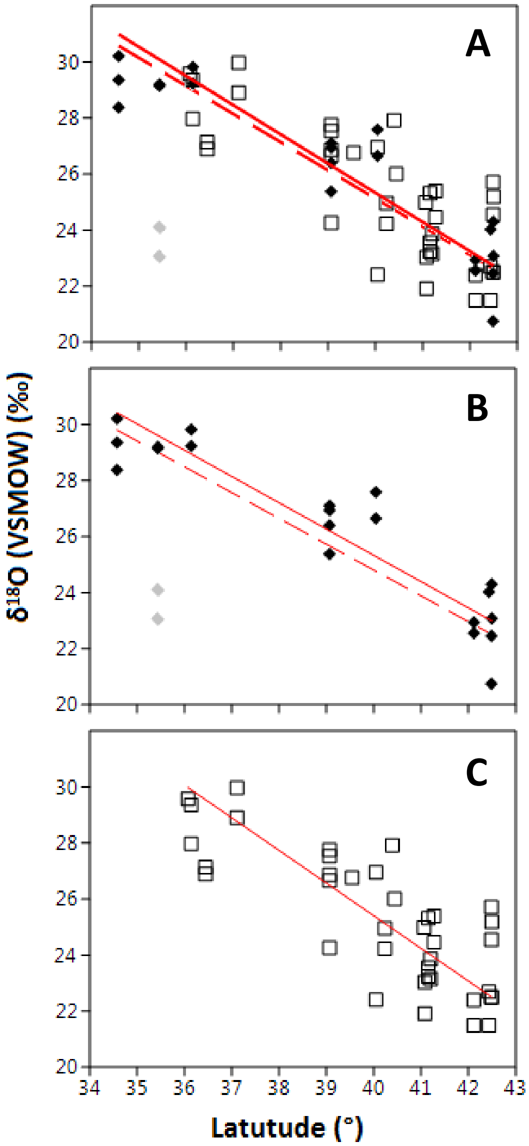

Figure 14. Relationship between latitude and $\delta^{18}O$ in rhinoceros tooth enamel. A: regression using all rhinoceros data, equations (2) and (6) in text. B: regression using only *Aphelops*, equations (3) and (5). C: regression using only *Teleoceras* data, equation (4). See text for equations. Open square = *Teleoceras*. Filled diamond = *Aphelops* samples. Gray filled diamond = *Aphelops* outliers. Solid line: regression line not including outliers. Dashed line: regression line including outliers.

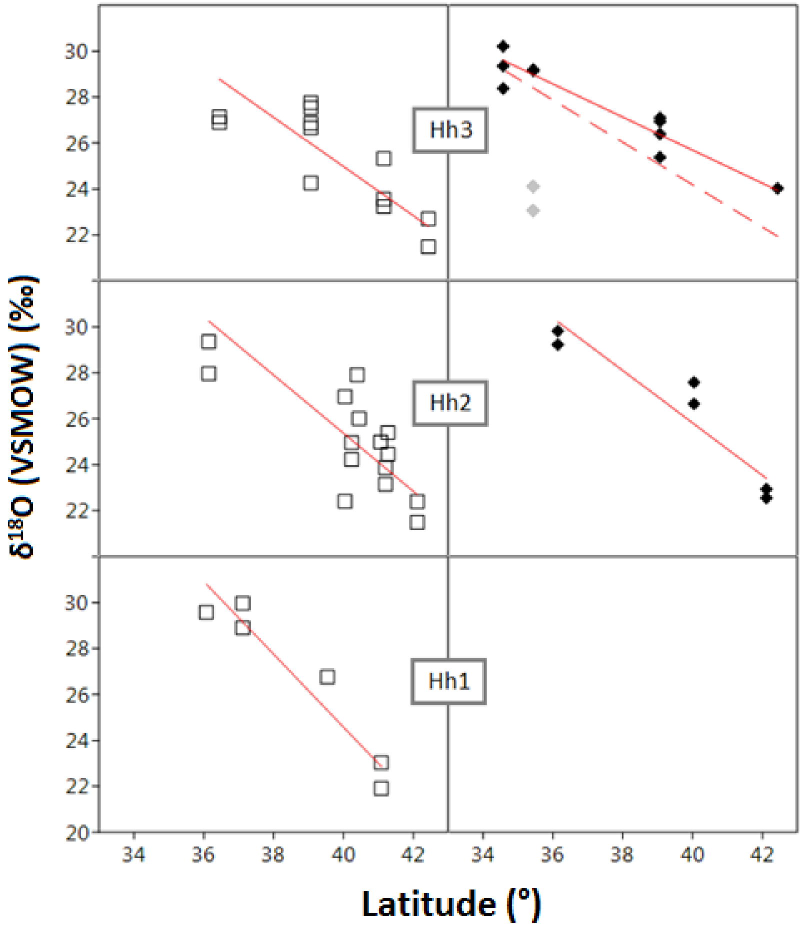

Figure 15. Relationship between latitude and tooth enamel $\delta^{18}O_E$ for each genus in each biochron. See Figure ## for symbols. Equations are as follows: Hh1 *Teleoceras*: $\delta^{18}O_E$ = -1.59(±0.23)*Latitude +87.99(±80.75) (r^2=0.91, p=0.003); Hh2 *Teleoceras*: $\delta^{18}O_E$ = -1.26(±0.23)*Latitude +75.96(±84.08) (r^2=0.58, p=0.001); Hh3 *Teleoceras*: $\delta^{18}O_E$ = -1.07(±0.20)*Latitude +67.76(±63.36) (r^2=0.65, p=0.002): Hh2 *Aphelops*: $\delta^{18}O_E$ = -1.14(±0.23)*Latitude +71.43(±63.20) (r^2=0.88, p=0.006); Hh3 *Aphelops* (all): $\delta^{18}O_E$ = -0.92(±0.25)*Latitude +61.07(±88.77) (r^2=0.24, p=0.104); Hh3 *Aphelops* (without outliers): $\delta^{18}O_E$ = -0.72(±0.08)*Latitude +54.49(±9.61) (r^2=0.89, p=0.000).

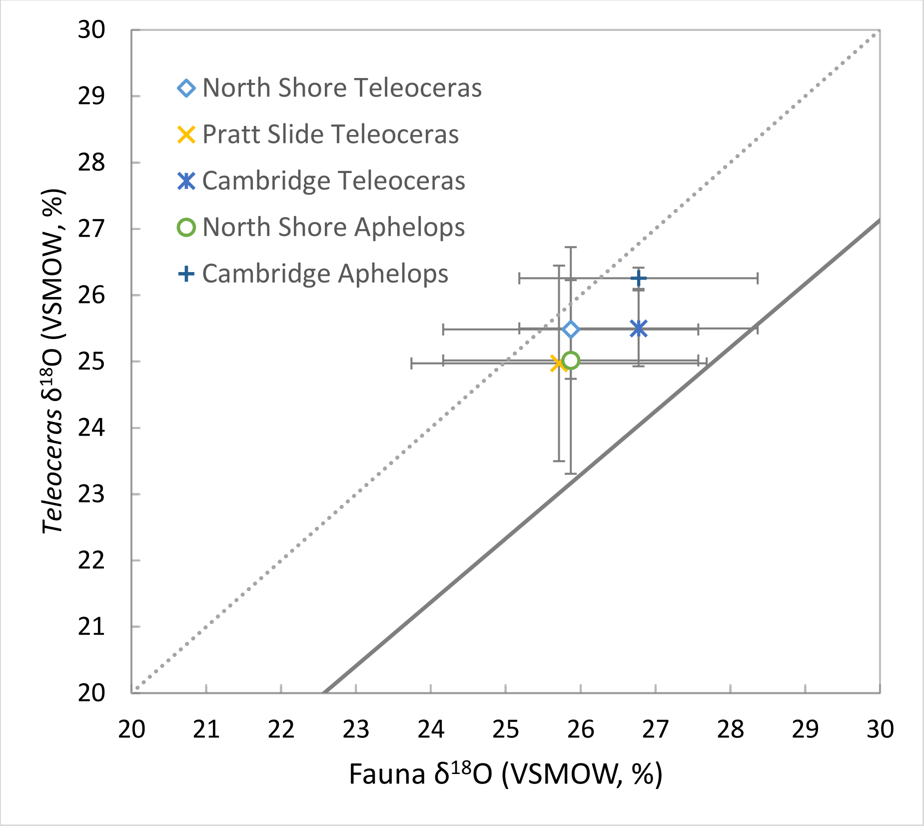

Figure 16. Bivariate plot of mean $\delta^{18}O_E$ values for rhinos and associated faunas.

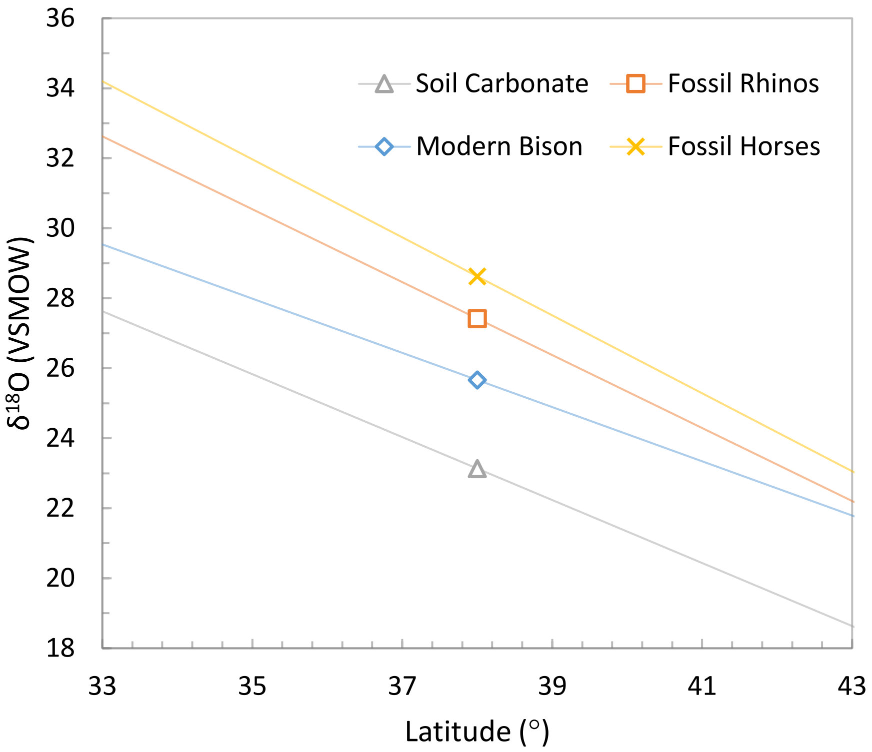

Figure 17. Regressions of oxygen values against latitude in the Great Plains using different proxies. Fossil rhino data are from this study. Modern bison data are from Hoppe (2006), the equation is: $\delta^{18}O_E$ = -0.77 (±0.02) * latitude + 55.10(±0.81), (r^2 = 0.996, p<0.001). Soil carbonate data are from Fox and Koch (2004), the equation is: $\delta^{18}O_E$ = -0.89 (±0.10) * latitude + 57.25 (±3.79), (r^2 = 0.87, p<0.001). Fossil horse data are from Passey et al (2002), the equation is: $\delta^{18}O_E$ = -1.13 (±0.08) * latitude + 71.33 (±10.66), (r^2 = 0.65, p<0.001). Equation for soil carbonate is calculated using Ordinary Least Squared regression, the rest are calculated using Reduced Major Axis regression.

Table 1. Numbers of localities by biochron. Uncertain biochron groups are noted with "*."

Biochron	Total localities	*Teleoceras* localities	*Aphelops* localities
Ba1	45	19	17
Ba2	133	42	20
Cl1	42	23	6
Cl2-3	182	111	31
*Cl or Cl2-3	5	3	1
Hh1	27	15	8
Hh2	24	19	14
Hh3	30	9	16
*Hh1 or Hh2	14	11	3
*Hh2 or Hh3	2	2	
*Hh3 or Hh4	1		
*Hh1 or Hh2 or Hh3 or Hh4	3	1	

Table 2. Summary statistics of *Aphelops* lower cheek teeth measurements by North American land mammal age. Linear dimensions in millimeters. Areal dimensions in square millimeters.

		Barstovian	Clarendonian	Hemphillian
m1L	N	32	13	37
	Mean	37.47	40.43	53.68
	S.E	0.48	1.08	0.64
	S.D	2.74	3.90	3.87
	Range	32.2 to 44.86	35.45 to 50.62	45.02 to 61.49
m1A	N	27	13	29
	Mean	1043.36	1263.92	2082.78
	S.E	19.88	60.61	47.35
	S.D	103.31	218.52	254.99
	Range	899.87 to 1352.08	1037.27 to 1936.72	1516.72 to 2493.05
m1-3 L	N	28	11	32
	Mean	121.89	130.38	167.91
	S.E	1.21	3.22	1.45
	S.D	6.42	10.67	8.21
	Range	108.21 to 135.77	119.1 to 157.23	146.46 to 181.88

Table 3. Summary statistics of *Aphelops* lower cheek teeth measurements by biochron. Linear dimensions in millimeters. Areal dimensions in square millimeters.

		Ba1	Ba2	Cl2-3	Hh1	Hh2	Hh3
m1L	N	25	7	13	3	12	22
	Mean	37.14	38.65	40.43	48.45	54.24	54.09
	S.E	0.45	1.53	1.08	2.92	1.22	0.67
	S.D	2.26	4.04	3.90	5.06	4.21	3.12
	Range	33.05 to 44.86	32.2 to 43.91	35.45 to 50.62	45.02 to 54.26	47.96 to 61.49	46.07 to 58.66
m1A	N	23	4	13	3	9	17
	Mean	1033.52	1099.95	1263.92	1600.59	2193.07	2109.49
	S.E	21.46	49.52	60.61	60.42	45.79	55.19
	S.D	102.92	99.04	218.52	104.65	137.38	227.56
	Range	899.87 to 1352.08	952.53 to 1165.36	1037.27 to 1936.72	1516.72 to 1717.87	2065.87 to 2478.66	1795.24 to 2493.05
m1-3L	N	21	7	11	2	10	20
	Mean	120.68	125.52	130.38	147.53	167.75	170.03
	S.E	1.01	3.66	3.22	1.07	2.00	1.46
	S.D	4.62	9.68	10.67	1.51	6.31	6.52
	Range	111.88 to 126.73	108.21 to 135.77	119.1 to 157.23	146.46 to 148.59	155.47 to 174.75	159.5 to 181.88

Table 4. Results of statistical tests for *Aphelops* measurements. Bold values indicate significant difference at 95%.

Variable	Comparison Groups	df	Student's *t*-test *p*
m1L	Ba1 vs. Ba2	1	0.20
m1L	Ba2 vs. Cl2-3	1	0.35
m1L	Cl2-3 vs. Hh1	1	**0.01**
m1L	Hh1 vs. Hh2	1	0.06
m1L	Hh2 vs. Hh3	1	0.91
m1L	Barstovian vs. Clarendonian	1	**0.01**
m1L	Clarendonian vs. Hemphillian	1	**0.00**
m1A	Ba1 vs. Ba2	1	0.24
m1A	Ba2 vs. Cl2-3	1	0.17
m1A	Cl2-3 vs. Hh1	1	**0.02**
m1A	Hh1 vs. Hh2	1	**0.00**
m1A	Hh2 vs. Hh3	1	0.33
m1A	Barstovian vs. Clarendonian	1	**0.00**
m1A	Clarendonian vs. Hemphillian	1	**0.00**
m1-3L	Ba1 vs. Ba2	1	0.08
m1-3L	Ba2 vs. Cl2-3	1	0.35
m1-3L	Cl2-3 vs. Hh1	1	0.051
m1-3L	Hh1 vs. Hh2	1	**0.00**
m1-3L	Hh2 vs. Hh3	1	0.37
m1-3L	Barstovian vs. Clarendonian	1	**0.00**
m1-3L	Clarendonian vs. Hemphillian	1	**0.00**

Table 5. Summary statistics of *Teleoceras* lower cheek teeth measurements by North American land mammal age. Linear dimensions in millimeters. Areal dimensions in square millimeters.

		Barstovian	Clarendonian	Hemphillian
m1L	N	32	71	79
	Mean	44.90	45.82	48.88
	S.E	0.85	0.50	0.49
	S.D	4.83	4.22	4.39
	Range	36.18 to 53.22	37.91 to 59.63	40.58 to 61.71
m1A	N	30	59	64
	Mean	1519.03	1466.25	1668.77
	S.E	37.29	23.57	25.69
	S.D	204.22	181.08	205.54
	Range	1118.50 to 1895.70	1171.25 to 2082.28	1208.53 to 2060.48
m1-3L	N	25	52	72
	Mean	147.96	154.13	163.22
	S.E	1.87	0.92	1.87
	S.D	9.33	6.67	15.88
	Range	128.73 to 163.99	142.67 to 169.43	110.79 to 189.04

Table 6. Summary statistics of *Teleoceras* lower cheek teeth measurements by biochron. Linear dimensions in millimeters. Areal dimensions in square millimeters.

		Ba1	Ba2	Cl1	Cl2-3	Hh1	Hh2	Hh3
m1L	N	18	14	8	63	35	36	8
	Mean	44.20	45.81	43.62	46.10	48.89	49.16	47.54
	S.E	1.10	1.36	1.06	0.54	0.70	0.79	1.38
	S.D	4.66	5.08	3.00	4.29	4.15	4.77	3.91
	Range	36.98 to 53.22	36.18 to 52.83	40.7 to 47.65	37.91 to 59.63	40.93 to 58.14	40.58 to 61.71	43.79 to 56.59
m1A	N	17	15	6	53	30	29	5
	Mean	1525.42	1510.66	1408.58	1472.78	1646.00	1717.69	1521.67
	S.E	48.67	60.10	63.00	25.27	36.62	38.12	78.02
	S.D	200.68	216.69	154.31	184.00	200.59	205.28	174.46
	Range	1126.67 to 1895.70	1118.50 to 1836.90	1309.70 to 1714.92	1171.25 to 2082.28	1208.53 to 2060.48	1378.33 to 2058.46	1299.25 to 1784.85
m1-3L	N	15	10	7	45	34	31	7
	Mean	147.16	149.14	154.22	154.11	159.39	168.00	160.67
	S.E	2.24	3.36	2.18	1.02	3.16	2.12	5.53
	S.D	8.67	10.62	5.77	6.86	18.42	11.79	14.63
	Range	132.88 to 161.34	128.73 to 163.99	146.48 to 161.46	142.67 to 169.43	110.79 to 182.11	143.36 to 189.04	144.73 to 187.97

Table 7. Results of statistical tests for *Teleoceras* measurements. Bold values indicate significant difference at 95%.

Variable	Comparison Groups	df	Student's *t*-test p
m1L	Ba1 vs. Ba2	1	0.36
m1L	Ba2 vs. Cl1	1	0.28
m1L	Cl1 vs. Cl2-3	1	0.12
m1L	Cl2-3 vs. Hh1	1	**0.00**
m1L	Hh1 vs. Hh2	1	0.80
m1L	Hh2 vs. Hh3	1	0.37
m1L	Barstovian vs. Clarendonian	1	0.33
m1L	Clarendonian vs. Hemphillian	1	**0.00**
m1A	Ba1 vs. Ba2	1	0.85
m1A	Ba2 vs. Cl1	1	0.32
m1A	Cl1 vs. Cl2-3	1	0.42
m1A	Cl2-3 vs. Hh1	1	**0.00**
m1A	Hh1 vs. Hh2	1	0.18
m1A	Hh2 vs. Hh3	1	0.053
m1A	Barstovian vs. Clarendonian	1	0.22
m1A	Clarendonian vs. Hemphillian	1	**0.00**
m1-3L	Ba1 vs. Ba2	1	0.61
m1-3L	Ba2 vs. Cl1	1	0.27
m1-3L	Cl1 vs. Cl2-3	1	0.97
m1-3L	Cl2-3 vs. Hh1	1	0.08
m1-3L	Hh1 vs. Hh2	1	**0.03**
m1-3L	Hh2 vs. Hh3	1	0.16
m1-3L	Barstovian vs. Clarendonian	1	**0.00**
m1-3L	Clarendonian vs. Hemphillian	1	**0.00**

Correlation of MAT and rhinoceros body size proxies.

Comparison Groups	df	*r*	*p*
MAT and *Teleoceras* m1L	6	-0.73	0.061
MAT and *Teleoceras* m1A	6	-0.35	0.442
MAT and *Teleoceras* m1-3L	6	-0.83	**0.021**
MAT and *Aphelops* m1L	5	-0.82	**0.045**
MAT and *Aphelops* m1A	5	-0.79	0.064
MAT and *Aphelops* m1-3L	5	-0.81	0.053

Table 8. Estimated mean body mass (kg) of *Aphelops* and *Teleoceras* through time. Estimates follow Damuth's (1990) equations for non-selenodont ungulates (D) and Janis' (1990) equations for perissodactyls and hyracoids (J).

Genus	Biochron	m1LD	m1LJ	m1AD	m1AJ	m1-3L
Aphelops	Ba1	1038.9	1850.4	980.9	1533.6	826.8
Aphelops	Ba2	1178.6	2100.6	1077.6	1685.5	931.2
Aphelops	Cl1	--	--	--	--	--
Aphelops	Cl2-3	1359.4	2424.8	1329.2	2080.7	1044.4
Aphelops	Hh1	2412.5	4316.4	1898.7	2976.4	1519.4
Aphelops	Hh2	3449.1	6182.9	3054.8	4797.7	2242.3
Aphelops	Hh3	3418.6	6128.0	2880.8	4523.3	2336.0
Teleoceras	Ba1	1802.8	3220.5	1765.7	2767.1	1508.1
Teleoceras	Ba2	2019.2	3609.2	1740.0	2726.6	1570.4
Teleoceras	Cl1	1729.5	3088.9	1565.5	2452.2	1738.0
Teleoceras	Cl2-3	2060.8	3684.0	1674.5	2623.6	1734.4
Teleoceras	Hh1	2482.5	4442.2	1980.7	3105.3	1920.5
Teleoceras	Hh2	2526.6	4521.6	2112.3	3312.6	2252.7
Teleoceras	Hh3	2271.1	4062.1	1759.2	2756.8	1967.9

Table 9. Results of statistical tests between *Aphelops* and *Teleoceras*. Bold values indicate significant different at 95%.

Variable	Time Interval	df	Student's *t*-test p
m1L	Ba1	1	**0.00**
m1L	Ba2	1	**0.00**
m1L	Cl1	--	--
m1L	Cl2-3	1	**0.00**
m1L	Hh1	1	0.86
m1L	Hh2	1	**0.00**
m1L	Hh3	1	**0.00**
m1L	Barstovian	1	**0.00**
m1L	Clarendonian	1	**0.00**
m1L	Hemphillian	1	**0.00**
m1A	Ba1	1	**0.00**
m1A	Ba2	1	**0.00**
m1A	Cl1	--	--
m1A	Cl2-3	1	**0.00**
m1A	Hh1	1	0.70
m1A	Hh2	1	**0.00**
m1A	Hh3	1	**0.00**
m1A	Barstovian	1	**0.00**
m1A	Clarendonian	1	**0.00**
m1A	Hemphillian	1	**0.00**
m1-3L	Ba1	1	**0.00**
m1-3L	Ba2	1	**0.00**
m1-3L	Cl1	--	--
m1-3L	Cl2-3	1	**0.00**
m1-3L	Hh1	1	0.38
m1-3L	Hh2	1	0.95
m1-3L	Hh3	1	**0.03**
m1-3L	Barstovian	1	**0.00**
m1-3L	Clarendonian	1	**0.00**
m1-3L	Hemphillian	1	0.12

Table 10. Temporal and geographic distribution of isotope samples. Dark gray indicates that there is no rhino locality from the state and time interval.

	Teleoceras					*Aphelops*				
	NE	CO	KS	OK	TX	NE	CO	KS	OK	TX
Hh1	2	▨	3	1			▨			
Hh2	11	2		▨	2	2	2		▨	2
Hh3	5	▨	5	2		1	▨	4		7
Hh4	5	▨	▨			4	▨	▨	▨	▨

Table 11. Summary statistics of carbon and oxygen isotope data.

	$\delta^{13}C$ (‰)					$\delta^{18}O$ (‰)				
	N	Mean	S. E.	S. D.	Range	N	Mean	S. E.	S. D.	Range
Hh1 *Teleoceras*	6	-8.4	0.2	0.5	-8.9 to -7.7	6	26.7	1.4	3.5	21.9 to 30.0
Hh2 *Teleoceras*	15	-9.1	0.3	1.0	-10.8 to -7.3	15	25.0	0.6	2.3	21.5 to 29.4
Hh3 *Teleoceras*	12	-8.8	0.3	1.2	-11.8 to -7.3	12	25.3	0.6	2.2	21.5 to 27.8
Hh4 *Teleoceras*	6	-10.0	0.4	1.0	-11.0 to -9.0	6	25.0	1.1	2.6	22.5 to 29.5
Hh2 *Aphelops*	6	-8.7	0.6	1.5	-10.0 to -5.9	6	26.5	1.3	3.1	22.6 to 29.8
Hh3 *Aphelops*	12	-10.1	0.6	2.2	-14.9 to -7.3	12	26.9	0.7	2.4	23.1 to 30.2
Hh4 *Aphelops*	4	-10.7	0.4	0.7	-11.6 to -10.0	4	22.7	0.7	1.5	20.8 to 24.3

Table 12. Results of statistical analyses testing for difference in isotopic values between *Aphelops* and *Teleoceras* at each time interval. Bold values indicate significant differences at 95% confidence level. Note that no *Aphelops* from Hh1 is sampled.

Variable	Comparison Groups	Mann-Whitney *U* test *p*
$\delta^{13}C$	*Aphelops* vs. *Teleoceras* in Hh2	0.97
$\delta^{13}C$	*Aphelops* vs. *Teleoceras* in Hh3	0.11
$\delta^{13}C$	*Aphelops* vs. *Teleoceras* in Hh4	0.46
$\delta^{13}C$	*Aphelops* vs. *Teleoceras* in Hh2-4	0.09
$\delta^{13}C$	*Teleoceras*, Hh1 vs. Hh2	0.09
$\delta^{13}C$	*Teleoceras*, Hh2 vs. Hh3	0.28
$\delta^{13}C$	*Teleoceras*, Hh3 vs. Hh4	0.051
$\delta^{13}C$	*Aphelops*, Hh2 vs. Hh3	0.15
$\delta^{13}C$	*Aphelops*, Hh3 vs. Hh4	0.30
$\delta^{18}O$	*Aphelops* vs. *Teleoceras* in Hh2	0.33
$\delta^{18}O$	*Aphelops* vs. *Teleoceras* in Hh3	0.11
$\delta^{18}O$	*Aphelops* vs. *Teleoceras* in Hh4	0.11
$\delta^{18}O$	*Aphelops* vs. *Teleoceras* in Hh2-4	0.19
$\delta^{18}O$	*Teleoceras*, Hh1 vs. Hh2	0.29
$\delta^{18}O$	*Teleoceras*, Hh2 vs. Hh3	0.81
$\delta^{18}O$	*Teleoceras*, Hh3 vs. Hh4	0.61
$\delta^{18}O$	*Aphelops*, Hh2 vs. Hh3	0.81
$\delta^{18}O$	*Aphelops*, Hh3 vs. Hh4	**0.02**

Table 13. Results of statistical analyses testing for difference in isotopic values between *Aphelops* and *Teleoceras* sampled from the same localities.

Variable	Locality	Mann-Whitney *U* test *p*
$\delta^{13}C$	*Aphelops* Draw	0.70
$\delta^{18}O$	*Aphelops* Draw	0.25
$\delta^{13}C$	Box T	0.70
$\delta^{18}O$	Box T	0.70
$\delta^{13}C$	Rhino Hill	0.90
$\delta^{18}O$	Rhino Hill	0.71
$\delta^{13}C$	Devil's Nest	0.82
$\delta^{18}O$	Devil's Nest	0.55