



Stable isotope paleoecology of White River ungulates during the Eocene–Oligocene climate transition in northwestern Nebraska

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ABSTRACT

We use the carbon and oxygen stable isotope content of mammalian tooth enamel to evaluate ancient biomes, habitat partitioning, and water use among 12 ungulate taxa from the White River Group in Nebraska. The White River Group spans an interval of climate change from the upper Eocene to the lower Oligocene when global climate cooled in a heterogeneous fashion. We test whether changes in biome structure or mammalian ecology occurred during this interval. We find that mean $\delta^{13}\text{C}$ values for both Eocene and Oligocene faunas are consistent with dry, open biomes (e.g., woodland-savanna or woody scrubland). A significant increase in mean faunal $\delta^{13}\text{C}$ values (+0.4‰) occurs in the lower Oligocene, primarily from the loss of individuals feeding in wetter–denser parts of the ecosystem. In the upper Eocene, *Megacerops* sp. (brontothere) and *Perchoerus probus* (peccary) have low mean $\delta^{13}\text{C}$ values consistent with feeding in wetter, denser habitats (presumably riparian), whereas significantly higher mean values in the cursorial horse, *Meshippus* spp., and the clawed oreodont, *Agriochoerus antiquus*, are consistent with feeding in more open, drier habitats. The extinctions of *Megacerops* sp. and *Trigonias* sp., a rhinocerotid with relatively low $\delta^{13}\text{C}$ values, along with a decrease in the abundance of *P. probus* and other taxa, suggests reduction in the extent of wet habitats in the Oligocene. The rare tapir *Colodon* sp. is the only taxon sampled with a mean $\delta^{13}\text{C}$ value low enough to indicate consistent feeding in a wet habitat in the Oligocene. However, range-through taxa occupy the same relative positions in isotopic space in both the Eocene and Oligocene faunas suggesting stability in drier habitats. A significant increase also occurs in mean faunal $\delta^{18}\text{O}$ values (+1.0‰) in the Oligocene, primarily from the loss or reduction in abundance of water dependent species. Variance in $\delta^{18}\text{O}$ values increases significantly in the Oligocene, which is consistent with greater water stress in plants from drier conditions. Oxygen values increase in *A. antiquus* (+0.9‰), the most aridity-sensitive species in both faunas, as expected for drier conditions, but values in another aridity-sensitive taxon (*Meshippus* spp.) are virtually unchanged. Together, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values generally suggest a shift to drier conditions in the early Oligocene although $\delta^{13}\text{C}$ values yielded more consistent results. The lack of a large negative shift in $\delta^{18}\text{O}$ values, expected with a decrease in mean annual temperature, suggests that any temperature changes in the early Oligocene were relatively small in the continental interior of North America.

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1. Introduction

The transition from an equable, warmer climate in the Eocene to a cooler Oligocene climate is often seen as one of the most significant intervals of climate change in the Cenozoic. Marine studies suggest that mid- to high-latitude ocean temperatures decreased globally by 5–6 °C over a geologically short interval of ~300 thousand years in the earliest Oligocene (Zachos et al., 2001, 2008; Liu et al., 2009; Miller et al., 2009). Cooling coincided with large-scale continental glaciation in Antarctica and with the modification of ocean circulation patterns (Coxall et al., 2005; Katz et al., 2008; Lear et al., 2008; Zachos et al., 2008; Miller et al., 2009). In the marine realm, many invertebrate

groups underwent major faunal turnover during this interval (e.g. Dockery and Lozouet, 2003; Nesbitt, 2003; Hansen et al., 2004; Pearson et al., 2008).

Studies of terrestrial sequences spanning the Eocene–Oligocene climate transition (EOCT) indicate that significant changes also occurred on the continents at mid-latitudes (Collinson, 1992; Evanoff et al., 1992; Legendre and Hartenberger, 1992; Retallack, 1992; Hooker, 1998; Myers, 2003; Hooker et al., 2004; Zanazzi et al., 2007), but that cooling was not uniformly distributed (Kohn et al., 2004; Grimes et al., 2005; Hooker et al., 2009). In Europe, for instance, cooling is associated with mammalian faunal turnover and immigration (Hooker et al., 2009), but in North America mammalian extinction rates were modest (Prothero and Heaton, 1996; Prothero, 1999; Alroy et al., 2000). A temperature drop as severe as 8.2 ± 3.1 °C was suggested for the mid-continent of North America (Zanazzi et al., 2007). However, most lines of evidence suggest increasing aridity with only minimal cooling

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(<2 °C). Evidence for increased aridity includes changes in soil structure and root trace size (Retallack, 1992; Terry, 2001), geochemical trends suggesting a ~300 mm decrease in mean annual precipitation (Sheldon and Retallack, 2004; Retallack, 2007; Sheldon, 2009; Sheldon et al., 2012), turnover in the terrestrial gastropod fauna (Evanoff et al., 1992), and a rapid decline of the aquatic herpetofauna (Hutchison, 1982, 1992); all of these are consistent with a change to a more open biome in the early Oligocene. Despite these corroborative proxies, several other studies indicate essentially no change in vegetation structure in Nebraska through this interval. Phytolith assemblages remain static (Strömberg, 2004, 2005) and a study using mammalian isotopes from six ungulate taxa suggested that mammalian habitats remained stable through the EOCT (Zanazzi and Kohn, 2008).

In this study we use the stable carbon and oxygen isotope compositions of a large diversity of mammalian ungulates from faunas before and after the EOCT to test the hypothesis that vegetation structure became more open in the early Oligocene in response to greater aridity. To accomplish this, we infer biomes and habitats for the late Eocene and early Oligocene by comparing fossil compositions to those predicted for various environments using the isotopic compositions of modern floras. The isotopic compositions of seven extinct genera from the upper Eocene and lower Oligocene are analyzed here for the first time, greatly increasing the diversity of mammal species studied from this interval. This allows us to test for habitat partitioning among a wider range of species than in the previous study (Zanazzi and Kohn, 2008) and provides more accurate mean isotopic values for the faunas. As in the previous study, the fossils used here come from the White River Group (WRG) in northwestern Nebraska (Fig. 1), although our fossils were collected from different areas, and may be from different stratigraphic levels (levels were not published in the previous study).

We expect that a shift to a more open biome in the early Oligocene will result in increased enamel carbon isotope values ($\delta^{13}\text{C}_\text{E}$) as some taxa shift to feeding in more open habitats or taxa occupying wetter-denser habitats are reduced in number or become extinct. We further expect that a shift to more arid conditions will result in an upward shift in enamel oxygen isotope values ($\delta^{18}\text{O}_\text{E}$) in aridity-sensitive species, relative to aridity-insensitive species, and that a marked decrease in mean annual temperature should result in a marked decrease in mean $\delta^{18}\text{O}_\text{E}$ faunal values.

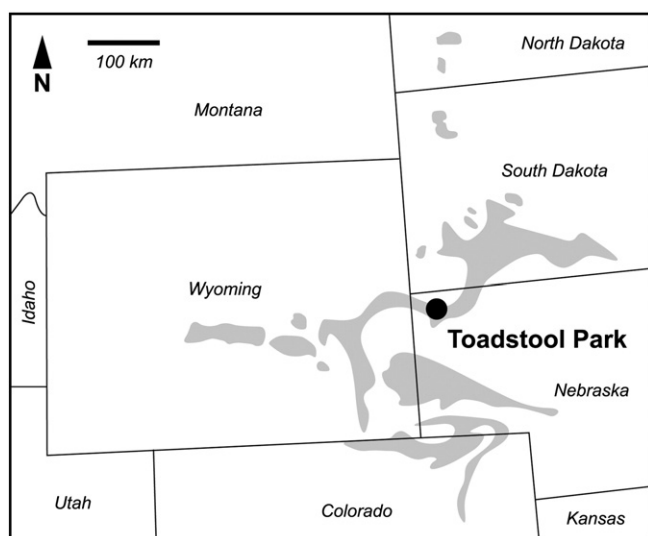


Fig. 1. Location map of the study area in northwestern Nebraska superimposed on WRG outcrops (in gray). Modified from Emry et al., 1987.

2. Stable isotopes in mammals as paleoecological proxies

2.1. Carbon isotopes in mammalian tooth enamel

The carbon isotope composition of mammalian tooth enamel is a direct reflection of an animal's diet, with predictable metabolic enrichment (Lee-Thorp and van der Merwe, 1987). Carbon isotope values in medium to large ungulates are typically enriched by ~13‰ to 14‰ above the vegetation they consume (Cerling and Harris, 1999; Passey et al., 2005). Pre-Miocene biomes in the North American mid-continent were dominated by vegetation using the C_3 photosynthetic pathway (Calvin cycle), with little or no influence from plants utilizing other photosynthetic pathways, such as CAM or C_4 (Cerling et al., 1993, 1997; Ehleringer and Monson, 1993; Tipton and Pagani, 2007; Secord et al., 2008; Zanazzi and Kohn, 2008; Edwards et al., 2010). Thus, we assume that the primary influence on $\delta^{13}\text{C}_\text{E}$ values in the WRG faunas was from C_3 vegetation. C_3 plants include most trees, shrubs, and high-altitude or high-latitude grasses. Modern C_3 plants have a global mean $\delta^{13}\text{C}$ value of ~−27‰ and range from −21‰ to −37‰ (O'Leary, 1988; Cerling and Ehleringer, 2000).

The wide range of $\delta^{13}\text{C}$ values exhibited by C_3 vegetation is largely the result of environmental factors that vary among habitats, such as availability of water and nutrients, and amount of solar radiation (O'Leary, 1988; Farquhar et al., 1989; van der Merwe and Medina, 1991; Ehleringer and Monson, 1993; Koch, 1998; Heaton, 1999). Generally, leaf $\delta^{13}\text{C}$ values increase under water-stressed conditions (Ehleringer et al., 1986; Stewart et al., 1995) and with increasing amounts of solar radiation, causing higher values in more sunlit areas (Ehleringer et al., 1986). A third factor is the recycling of ^{13}C -depleted CO_2 under forest canopies, resulting in lower $\delta^{13}\text{C}$ leaf values (van der Merwe and Medina, 1991). Together these factors result in the most negative $\delta^{13}\text{C}$ values for C_3 plants occurring in closed canopy biomes, such as rainforests, and the most positive ones in dry open canopy biomes, such as woody scrublands (Farquhar et al., 1989; Stewart et al., 1995). The patterns seen in plant $\delta^{13}\text{C}$ values are reflected in mammalian herbivore consumers, which provide a useful proxy for inferring ancient biomes, and habitat use within those biomes (Ambrose and DeNiro, 1986; Cerling and Harris, 1999; Cerling et al., 2004; Feranec, 2007).

2.2. Oxygen isotopes in mammalian tooth enamel

The oxygen isotope composition of mammalian tooth enamel can be used to infer drinking behavior and habitat preference for a taxon, as well as local climatic conditions such as humidity (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 factors influencing the $\delta^{18}\text{O}$ composition of mammalian bioapatites have been considered in detail elsewhere (Bryant and Froelich, 1995; Kohn, 1996), and will be described only briefly here. 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. Because most mammals maintain a fairly constant body temperature of ~37 °C, variation in $\delta^{18}\text{O}_\text{E}$ values among taxa is caused primarily by behavioral and physiological differences centering on whether or not the animal obtains most of its water from drinking or from its food (Bryant and Froelich, 1995; Kohn, 1996).

Water-dependent taxa (i.e., frequent or obligate drinkers) should have $\delta^{18}\text{O}$ values more reflective of local drinking water (Bryant and Froelich, 1995; Kohn, 1996). These taxa, which are insensitive to ^{18}O -enrichment from the evaporation of leaf water or from physiological factors, have been called aridity-insensitive (EI taxa; Levin et al., 2006). In contrast, those that are less reliant on drinking and/or that get a significant part of their water from leaves are aridity-sensitive (ES taxa; Levin et al., 2006). In general, the highest $\delta^{18}\text{O}$ values in leaf water are expected to occur in open areas with high

irradiance because of higher rates of evapotranspiration at the leaf surface, and the lowest values in more densely vegetated areas (Quade et al., 1995; Cerling et al., 2004; Feranec and MacFadden, 2006).

3. Materials and methods

The White River Group in northwestern Nebraska contains a rich record of superposed mammalian faunas during the latest Eocene and early Oligocene epochs. Fossils used here come from exposures of the Big Cottonwood Creek Member (BCCM) of the upper Chadron Formation and the Orella Member of the lower Brule Formation of the WRG in and around Toadstool Geologic Park, northwestern Nebraska (Fig. 1). Faunas from the former units were the original basis for the Chadronian and Orellan North American Land Mammal “ages” (Wood et al., 1941; Woodburne, 1987, 2004 volumes). The boundaries for these informal “ages” are based on the first occurrences of mammal species and thus are not synchronous with the boundaries of the similarly named lithologic units (Fig. 2). Current durations for the “ages” are ~37.0–33.7 Ma for the Chadronian (late Eocene) and ~33.7–32.0 Ma for the Orellan (earliest Oligocene; Prothero and Emry, 2004).

A total of 114 samples from twelve genera (Table 1) of WRG ungulates were analyzed for this study (Appendix A) – seven of them (*Colodon* sp., *Hyracodon nebraskensis*, *Perchoerus probus*, *Eotylopus reedi*, *Archaeotherium mortoni*, *Aepinacodon americanum*, and *Agriocherus antiquus*) for the first time. The other five (except *Trigonias* sp.) were

previously sampled by Zanazzi and Kohn (2008) from localities in the Toadstool Park area not represented in the University of Nebraska State Museum (UNSM) collections. We sampled mostly common taxa in order to get a good average representation of the environment, but we also sampled a few rare species in an attempt to include a wide range of habitats. Several taxa were sampled only from the Chadronian either because they were extinct by the Orellan (*Megacerops* sp., *Trigonias* sp., and *E. reedi*) or they became rare in the Orellan (*A. americanum* and *P. probus*), in spite of a much larger Orellan collection. The tapir *Colodon* sp. is not present in the Chadronian collection at UNSM and is rare in the Orellan collection. The other six taxa (*Mesohippus* spp., *H. nebraskensis*, *Subhyracodon* sp., *Merycoidodon* sp., *A. antiquus*, and *A. mortoni*) were sampled from both the Chadronian and Orellan. Table 1 includes a summary of suggested diets and habitats for these taxa at the generic level based on published studies. All specimens are curated at UNSM.

Most specimens used in this study were collected by parties from UNSM led by Schultz and Stout. Schultz and Stout (1955) established a series of loosely characterized, local “zones” for the White River Group (Fig. 2). Although the utility of the Schultz and Stout zones has been questioned (e.g., Prothero and Emry, 2004; Zanazzi et al., 2009), the stratigraphic distance of specimens collected by Schultz and Stout above or below marker beds (especially the upper purplish white [UPW] a dated volcanic ash) was often precisely recorded in field notes, allowing us to place many of these specimens into a well-resolved, sub-meter level, stratigraphic context. When coupled with the recognition of paleomagnetic zones (Prothero and Swisher, 1992) and age estimates from volcanic ashes (Obradovich et al.,

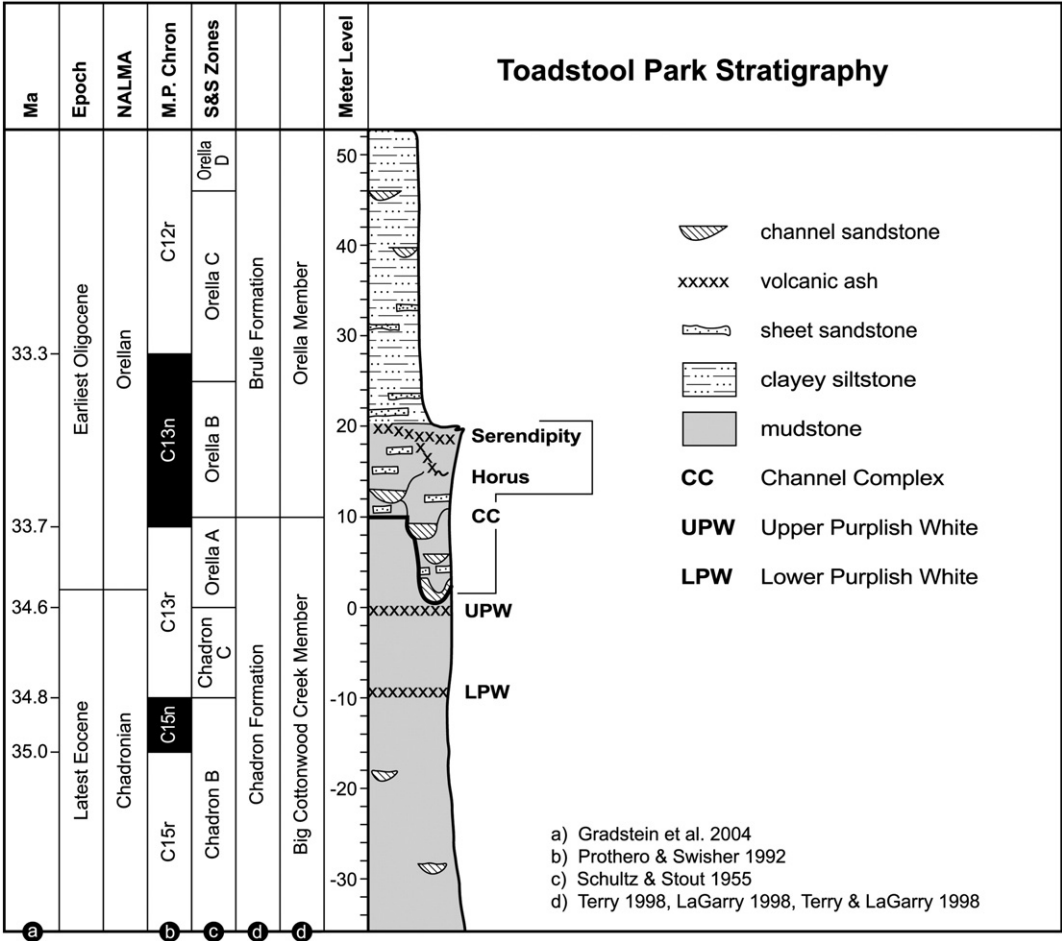


Fig. 2. Chrono- and lithostratigraphy of the Toadstool Park stratigraphic section. Volcanic ash dates from Zanazzi et al. (2009). Lithostratigraphy is modified from Grandstaff and Terry (2009). Abbreviations: Ma, million years before present; M.P., magnetic polarity; NALMA, North American Land-Mammal “age”; S&S, Schultz and Stout zones. Data from Gradstein et al. (2004), LaGarry (1998), Terry (1998), and Terry and LaGarry (1998).

Table 1

Summary of the latest hypothesized habitat preferences and diets of the studied White River ungulates.

Genus	Est. body mass	Dentition	Habitat	Diet
<i>Perissodactyls</i>				
<i>Mesohippus</i>	42–54 kg (1)	Brachy-lophodont; molariform premolars (1)	Woodlands (7, si)	Browser (1, mp; 20, mw), mixed-feeder/grazer (10, mc; 17, mc)
<i>Hyracodon</i>	160 kg (2)	Brachy-lophodont (3)	Open plains (3)	Browser (3, mp; 10, mc)
<i>Subhyracodon</i>	500 kg (2)	Brachy-lophodont (3)	Open plains (7, si)	Mixed-feeder (3), browser (10)
<i>Trigonias</i>	500 kg (2)	Brachy-lophodont (3)	Open plains (7, si)	Mixed-feeder (3, 10)
<i>Colodon</i>	150 kg (2)	Bilophodont (15)	Forest (16)	Browser (10)
<i>Megacerops</i>	1900 kg (2)	Brachy-selenodont (4)	Forest (7, si)	Browser (9, mc), mixed-feeder (10, mc)
<i>Artiodactyls</i>				
<i>Archaeotherium</i>	180 kg (2)	Robust, apically worn premolars; bunodont molars (5)	Woodlands/open plains (5)	High abrasion omnivore (5, mc/mp; 10, mw)
<i>Agriochœrus</i>	40–50 kg (18, 19)	Brachy-selenodont (6)	Forest/open plains (8)	Browser (11, mp), mixed-feeder (10, mc)
<i>Merycoidodon</i>	50 kg (2)	Brachy-selenodont (6)	Woodlands (7, si)	Browser/mixed feeder (11, mp), grazer (10, mc)
<i>Perchoerus</i>	35 kg (2)	Bunodont (14)	Riparian/open plains (8, sed)	Hard object browser (10, mc)
<i>Eotylpus</i>	20 kg (2)	Buno-selenodont (13)	Forest (13)	Mixed-feeder (10, mc)
<i>Aepinacodon</i>	280 kg (2)	Brachy-selenodont (12)	Semi-aquatic (12, sed)	Mixed-feeder (10, mc)

Habitat and diet interpretations based on: (mw = mesowear; mc = microwear; si = stable isotopes; mp = morphology; sed = sedimentology). References: (1) MacFadden (1987); (2) Mendoza et al. (2006); (3) Mead and Wall (1998a, b); (4) Rose (2006); (5) Joeckel (1990); (6) Stevens and Stevens (1996); (7) Zanazzi and Kohn (2008); (8) Clark et al. (1967); (9) Muhlbachler and Solounias (2002); (10) Dewar (2008); (11) Wall and Shikany (1995); (12) Kron and Manning (1998); (13) Prothero (1998); (14) Wright (1998); (15) Colbert and Schoch (1998); (16) DeSantis and MacFadden (2007); (17) Solounias and Semperebon (2002); (18) Radinsky (1978); (19) Janis (1982); (20) Muhlbachler et al. (2011).

1995), the UNSM collections can be placed in a strong geochronologic framework (Fig. 2).

Of particular interest to our study is the placement of the Eocene–Oligocene (E–O) boundary, and the EOCT. Based on previous work both the E–O boundary and the most rapid interval of cooling during the EOCT should occur in the upper part of polarity zone C13r, locally in “Orella A” of Schultz and Stout (Fig. 2). The Chadronian–Orellan boundary is approximately coincident with the E–O boundary, following the biostratigraphy of Zanazzi et al. (2009). The Chadronian–Orellan had long been defined by the last appearance of brontotheres (Wood et al., 1941) but this definition has subsequently been challenged due to claimed diachrony of these last appearances among WRG exposures in Wyoming and Nebraska (Prothero and Whittlesey, 1998). The boundary was redefined by Prothero and Whittlesey (1998) based on the first appearances of *Hypertragulus calcaratus*, *Leptomeryx evansi*, and *Poebrotherium wilsoni*. Due to unresolved issues with sampling and possible minor diachrony of these first appearances at Toadstool Park, Zanazzi et al. (2009) conservatively placed the Chadronian–Orellan boundary at 2 ± 5 m above the UPW, which we follow here (Fig. 2).

3.1. Sample treatment and statistical analysis

Isotopic sampling was done under a binocular microscope using a mounted, variable speed dental drill. Enamel powder (3–4 mg) was drilled from each tooth along a non-occlusal surface perpendicular to the growth axis using a 1 mm diamond burr. Care was taken to avoid decalcified or fractured enamel. Pretreatment followed Koch et al. (1997) except that samples were placed in a drying oven overnight at 60 °C to remove water, rather than being lyophilized. Samples were reacted with 2–3% reagent grade NaOCl for 24 h to remove organic matter, rinsed five times with distilled water, and dried. Nonstructural carbonates were then removed by reacting samples in 1.0 M buffered acetic acid for 24 h. This was again followed by rinsing and drying.

To avoid a potential bias from nursing, third molars, which form after weaning in extant eutherian mammals, were preferentially sampled. When third molars were not available, other late erupting teeth (e.g., fourth premolars, second molars) were sampled. The sampling of a single tooth position can also help to reduce variability from seasonal fluctuations in the $\delta^{18}\text{O}$ values of precipitation (e.g., Secord et al., 2010). This assumes that a species followed seasonal birthing cycles and that single teeth formed over only part of a year. These

assumptions should be reasonable based on modern analogs of mammals in temperate climates (e.g., Hillson, 1986). Reducing seasonal variability in $\delta^{18}\text{O}$ values is desirable for comparing changes in $\delta^{18}\text{O}$ values between different time intervals, but could cause isotopic separation among contemporaneous taxa biasing habitat interpretations. However, because of attenuation that takes place due to protracted mineralization (e.g., Passey et al., 2002) maximum seasonal differences in oxygen in serially sampled teeth are usually not more than a few per mil, and bulk sampling further attenuates seasonality. Moreover, we differentiate habitats primarily using differences in mean $\delta^{13}\text{C}_\text{E}$ values, and annual variability in carbon is relatively small in most serially sampled teeth from C_3 environments (Higgins and MacFadden, 2004; Nelson, 2005; Zanazzi and Kohn, 2008; Feranec et al., 2009). Zanazzi and Kohn (2008) serially sampled teeth of *Subhyracodon* sp. from the Toadstool area and showed that seasonal variability in $\delta^{13}\text{C}_\text{E}$ values was very low. They concluded that variation in tooth position was of little concern for habitat interpretation in WRG mammals, with which we concur.

Isotopic measurements were done at the University of Michigan Stable Isotope Laboratory (UMSIL). Samples were reacted with phosphoric acid for 17 min at 77 ± 1.0 °C in a Finnigan MAT Kiel IV preparation device. Isotopic ratios of the resultant CO_2 were measured using a Finnigan MAT 253 triple collector isotope ratio mass spectrometer. Analytical precision at UMSIL is better than $\pm 0.1\%$ (1 standard deviation) for both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values, based on international standards for carbonate (NBS-18, NBS-19) (Lora Wingate, lab manager – personal communication). Intra-lab enamel standards (LOX, from the African elephant, courtesy of D. L. Fox; MES-1, from fossil mammoth enamel) were used to monitor variance among batches. Mean values and variances were: $\delta^{18}\text{O} = 31.89 \pm 0.11\%$ and $\delta^{13}\text{C} = -5.65 \pm 0.02\%$ (95% confidence, $n = 16$) for LOX and $\delta^{18}\text{O} = 23.07 \pm 0.09\%$ and $\delta^{13}\text{C} = -9.63 \pm 0.02\%$ (95% confidence, $n = 16$) for MES-1.

Isotopic results are expressed in standard δ -notation: $X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is the $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ value, and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{18}\text{O}/{}^{16}\text{O}$, respectively. The $\delta^{13}\text{C}$ values are reported relative to the Vienna PeeDee Belemnite (VPDB) standard and $\delta^{18}\text{O}$ values are reported here relative to the Vienna Standard Mean Ocean Water (VSMOW) standard. All errors on mean values are reported with 95% confidence of the mean (1.96*standard error) unless otherwise stated.

We performed a pairwise comparison of all genera in each fauna represented by two or more isotope values using Fisher's LSD test and Tukey's post hoc test. Tukey's test adjusts the level of significance by accounting for the number of pairs compared. In all cases, our use

of “significance” refers to a probability of $\leq 5\%$ ($p \leq 0.05$) that the two compared mean values were drawn from the same population and are not significantly different. Welch’s F-test was utilized for comparisons in which variances were significantly different; results for this test are noted in instances where its use was required. In cases where samples were not normally distributed the non-parametric Kruskal–Wallis test was used.

Mean values for faunal samples were also compared pair-wise to means for each of the predicted biomes to test for significant differences using the abovementioned tests. The same was done for taxa overlapping the ranges of predicted habitats. All uses of “significance” in text refer to statistical significance at $p \leq 0.05$ unless otherwise noted.

3.2. Habitat modeling

We follow the approach of Secord et al. (2008) for interpreting biomes and habitats in the White River Group (habitats and microhabitats, respectively, as used by Secord et al., 2008). In this study “biome” is used to characterize the general aspect of local vegetation structure, such as open or closed canopy, whereas “habitat” refers to areas within a biome, such as the understory in a closed canopy forest, or the riparian strip in a woodland-savanna biome. This approach uses plant $\delta^{13}\text{C}$ values from a variety of modern biomes. The modern biomes used here were chosen because they had similar sampling protocols, sampled a diversity of species, were reflective of intra-biome diversity, and they provided data from both wet and dry seasons that could be used to calculate a representative mean annual value. Mean $\delta^{13}\text{C}$ values were normalized to parameters for the latest Eocene/earliest Oligocene of Nebraska. Factors that were considered were: (1) the effects of latitude and altitude on $\delta^{13}\text{C}$ values in vegetation; (2) diet–enamel enrichment; and (3) changes in the composition of atmospheric CO_2 ($\delta^{13}\text{C}_\text{A}$) between the latest Eocene/earliest Oligocene and the present. We assume an average diet-to-enamel enrichment factor for WRG ungulates of 14.1‰ based on enrichment factors in extant ungulates calculated by Cerling and Harris (1999). Atmospheric carbon in the latest Eocene and earliest Oligocene was $\sim 0.5\%$ more positive than during the pre-industrial Holocene based on the dataset of Tipler et al. (2010). When considering the 1.5‰ decrease in $\delta^{13}\text{C}_\text{A}$ values caused by industrialization over the last two centuries (Friedli et al., 1986), the latest Eocene/earliest Oligocene $\delta^{13}\text{C}_\text{A}$ value was $\sim 2.0\%$ more positive than now. The total adjustment between normalized modern plant $\delta^{13}\text{C}$ values and WRG ungulate $\delta^{13}\text{C}_\text{E}$ values is +16.1‰. Model results indicate the following boundaries and ranges for mean $\delta^{13}\text{C}_\text{E}$ values from Chadronian and Orellan ungulates: closed canopy biomes (tropical rainforests and monsoon forests): $\leq -12.2\%$; open canopy biomes (woodland-savannas, woody scrublands, seasonally dry forests, and C_3 grasslands): $< -12.2\%$ to -6% ; and mixed C_3/C_4 biomes: $> -6\%$. The upper boundary for C_3 vegetation represents very dry, water-stressed biomes.

3.3. Aridity proxies

Levin et al. (2006) developed an “aridity index” for calculating differences in water deficit (WD) among faunas as a proxy for differences in environmental humidity. The aridity index uses the difference in mean $\delta^{18}\text{O}_\text{E}$ values between mammal species that were either aridity-sensitive (ES) or aridity-insensitive (EI). EI species are expected to track meteoric water values while ES species are sensitive to changes in humidity. The difference between mean values for EI and ES species is expected to increase with greater aridity as $\delta^{18}\text{O}$ values in ES species increase with greater aridity. We chose *Archaeotherium mortoni* as the ES species since it was almost certainly an omnivore based on its brachydont and bunodont dentition (Table 1), and has a low mean $\delta^{18}\text{O}_\text{E}$ value relative to the rest of the fauna. We chose *Agriochoerus antiquus* as our ES species because it has the highest

mean $\delta^{18}\text{O}_\text{E}$ value in the fauna, which is significantly elevated above many other taxa. Difference in Water Deficit (ΔWD), proportional to differences in humidity between two faunas, was determined using the following equation from Levin et al. (2006):

$$\Delta\text{WD} = \Delta\epsilon_{\text{ES-EI}} / 5.01 \times 10^{-3} \quad (1)$$

where ΔWD is change in water deficit in mm/year between two faunas, $\Delta\epsilon_{\text{ES-EI}}$ is the difference in mean $\delta^{18}\text{O}_\text{E}$ values between ES and EI taxa between two faunas, and 5.01×10^{-3} is the slope ($\text{SE } 1.98 \times 10^{-3}$) of the relationship between ES and EI species, calculated empirically from extant mammals. Ideally 10 specimens of *A. mortoni* and 10 of *A. antiquus* would be needed for both the Chadronian and Orellan faunas to determine fairly precise changes in water deficit (Levin et al., 2006). The recommended sample sizes could not be met for this study so uncertainty in estimates is fairly large.

We also utilized the general herbivore (#17) and the Dik-dik (#24) equations from Kohn (1996), to estimate changes in relative humidity using changes in mean faunal $\delta^{18}\text{O}_\text{E}$ values and changes in our aridity sensitive species (*Agriochoerus antiquus*), respectively.

4. Results

4.1. Isotopic changes across the EOCT

Significant increases of 0.4‰ ($p = 0.038$, Fisher’s LSD) and 1.0‰ ($p = 0.012$, Welch’s F-test) occur in faunal $\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$ values, respectively, from the Chadronian to the Orellan. These increases are caused primarily by Chadronian taxa with low $\delta^{13}\text{C}_\text{E}$ and/or low $\delta^{18}\text{O}_\text{E}$ values that are no longer present in the Orellan, or that were not sampled in the Orellan because of decreased abundance, as discussed below. When all samples from only range-through taxa are considered, mean $\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$ values increase by 0.2‰ and 0.4‰, respectively, but neither change is significant ($p = 0.328$, Fisher’s LSD; $p = 0.183$, Welch’s F-test, respectively). Changes in individual range-through taxa are also not significant with 95% confidence but increases in $\delta^{13}\text{C}_\text{E}$ values in *Hyracodon nebraskensis* and $\delta^{18}\text{O}_\text{E}$ values in *Agriochoerus antiquus* are significant with 90% confidence (+0.8‰, $p = 0.075$, Fisher’s LSD; +0.9‰, $p = 0.078$, Kruskal–Wallis; respectively). The *A. antiquus* sample from the Orellan is highly skewed by a single negative outlier (22.5‰, Appendix A), however, and removal of this outlier results in a significant ($p = 0.032$, Fisher’s LSD) increase of 1.5‰ in *A. antiquus* $\delta^{18}\text{O}_\text{E}$ values. *A. antiquus* is important since it has the highest $\delta^{18}\text{O}_\text{E}$ values in both faunas and is the strongest candidate for an aridity-sensitive taxon.

4.2. Chadronian and Orellan biomes in northwestern Nebraska

Fig. 3 shows that both Chadronian and Orellan faunal means plot in the range expected for dry, open canopied C_3 biomes with annual precipitation ranging from ~ 300 –500 mm. Both means are significantly different than those predicted for “wet” biomes receiving > 800 mm of precipitation, ranging from wet woodland-savanna to closed canopy rainforests but are indistinguishable from “dry” biomes such as dry woodland-savanna, woody scrublands, grasslands, and seasonally dry forests (Table 4A). A comparison of the Chadronian and Orellan faunas (Fig. 4, Tables 2 & 3) shows that mean $\delta^{13}\text{C}_\text{E}$ values for individual taxa in the Orellan fauna are all -9.3% or higher, with the exception of the rare tapir, *Colodon* sp. (-12.2%). This contrasts with the Chadronian fauna, in which five taxa (*Hyracodon nebraskensis*, *Subhyracodon* sp., *Trigonias* sp., *Megacerops* sp., and *Perchoerus probus*) have mean $\delta^{13}\text{C}_\text{E}$ values that plot in the range between -9.7% and -10.9% . Thus, an isotopic “gap” is present in the Orellan fauna, previously filled by several taxa in Chadronian fauna. This gap represents relatively wetter–denser habitats. Notably, the taxa that fill this “gap” in the Chadronian become extinct or decrease in abundance in the Orellan.

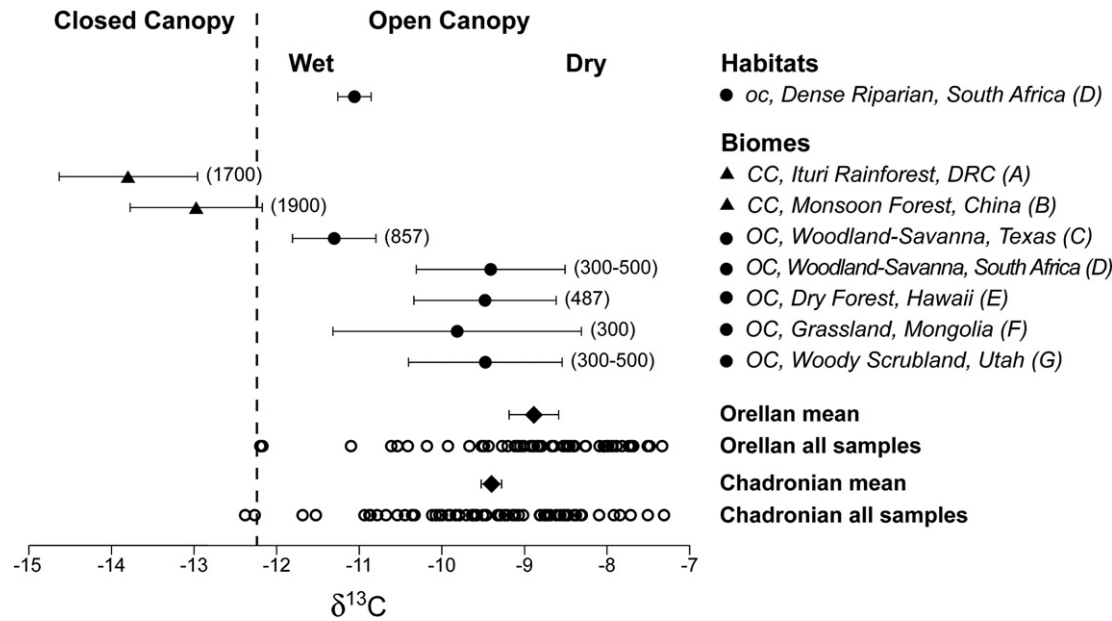


Fig. 3. Predictive model for $\delta^{13}\text{C}_\text{E}$ values from different biomes and habitats in the late Eocene (Chadronian) and early Oligocene (Orellan). Predictions are based on $\delta^{13}\text{C}$ values from modern floras normalized to 42° N latitude, an altitude of 1.10 km (Sjostrom et al., 2006), and corrected for diet–enamel enrichment and change in atmospheric $\delta^{13}\text{C}$ values (see text). Solid triangles (closed canopy) and circles (open canopy) show mean $\delta^{13}\text{C}_\text{E}$ values expected for a diverse sampling of mammalian herbivores. Mean annual precipitation values (mm/year) for modern biomes (listed on right) used to make predictions are given in parentheses next to error bars. Solid diamonds show uncorrected mean values and open circles show individual values for the Chadronian and Orellan faunas. All error bars show 95% confidence of mean ($\pm 1.96 \cdot \text{SE}$). CC = closed canopy (black triangles), OC = open canopy (black circles). Data sources: A, Cerling et al., 2004; B, Ehleringer et al., 1987; C, Jessup et al., 2003; D, Codron et al., 2005; E, Sandquist and Cordell, 2007; F, Cerling and Harris, 1999; G, Williams and Ehleringer, 1996.

Table 2

A. Descriptive statistics for Chadronian ungulate taxa examined in this study. B. Matrices of pairwise probabilities of mean differences in $\delta^{13}\text{C}_\text{E}$ (top) and $\delta^{18}\text{O}_\text{E}$ (bottom) values among Chadronian ungulate taxa. Values shown in bold indicate significance for $\alpha \leq 0.05$ using Fisher's least significant difference tests. Pairs that were also significant using Tukey's post hoc test are indicated by asterisks (* $\alpha \leq 0.05$).

A. Chadronian genus	n	Mean $\delta^{13}\text{C}_\text{E}$ (‰, VPDB)	S.D. (‰)	S.E. (‰)	Range (‰)	Mean $\delta^{18}\text{O}_\text{E}$ (‰, VSMOW)	S.D. (‰)	S.E. (‰)	Range (‰)
<i>Mesohippus</i> spp.	12	−8.4	0.6	0.2	−9.5 to −7.3	24.0	0.9	0.2	22.4 to 25.0
<i>Hyracodon nebraskensis</i>	7	−9.7	0.7	0.3	−10.3 to −8.7	25.2	1.5	0.6	23.5 to 27.2
<i>Subhyracodon</i> sp.	2	−9.8	0.9	0.7	−10.5 to −9.1	22.0	0.0	0.0	22.0
<i>Trigonias</i> sp.	7	−9.8	0.6	0.2	−10.8 to −9.2	23.0	1.1	0.4	21.2 to 24.9
<i>Megacerops</i> sp.	7	−10.9	0.9	0.4	−12.3 to −9.8	23.0	0.5	0.2	22.4 to 23.6
<i>Archaeotherium mortoni</i>	6	−9.4	0.8	0.3	−10.4 to −8.5	21.9	1.7	0.7	20.5 to 25.2
<i>Agriochoerus antiquus</i>	3	−8.4	0.5	0.3	−8.8 to −7.8	26.1	0.6	0.3	25.5 to 26.7
<i>Merycoidodon</i> sp.	8	−9.1	0.6	0.2	−9.7 to −8.1	23.3	2.5	0.9	19.2 to 26.4
<i>Aepinacodon americanum</i>	5	−8.9	1.2	0.5	−10.7 to −7.5	22.3	0.4	0.2	21.8 to 22.6
<i>Eotylpus reedi</i>	4	−9.1	0.5	0.2	−9.6 to −8.6	21.7	1.4	0.7	20.4 to 23.1
<i>Perchoerus probus</i>	6	−10.3	1.2	0.5	−12.3 to −9.1	21.8	0.9	0.4	20.5 to 22.6
Chadronian fauna	67	−9.4	1.1	0.1	−12.3 to −7.3	23.2	1.7	0.2	19.2 to 26.7

B. Chadronian $\delta^{13}\text{C}_\text{E}$, $\delta^{18}\text{O}_\text{E}$	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
1. <i>Mesohippus</i> spp.	1.00, 1.00										
2. <i>H. nebraskensis</i>	0.000* , 0.035*	1.00, 1.00									
3. <i>Subhyracodon</i> sp.	0.0097* , 0.007*	0.815, 0.020*	1.00, 1.00								
4. <i>Trigonias</i> sp.	0.000* , 0.044*	0.721, 0.008*	0.965, 0.227	1.00, 1.00							
5. <i>Megacerops</i> sp.	0.000* , 0.014*	0.019* , 0.003*	0.204, 0.015*	0.025* , 0.976	1.00, 1.00						
6. <i>A. mortoni</i>	0.005* , 0.003*	0.534, 0.003*	0.551, 0.943	0.307, 0.169	0.010* , 0.111	1.00, 1.00					
7. <i>A. antiquus</i>	0.981, 0.001*	0.022* , 0.325	0.106, 0.002*	0.005* , 0.002*	0.003* , 0.000*	0.068, 0.005*	1.00, 1.00				
8. <i>Merycoidodon</i> sp.	0.015* , 0.351	0.103, 0.093	0.191, 0.496	0.031* , 0.817	0.001* , 0.260	0.374, 0.085	1.00, 1.00				
9. <i>A. americanum</i>	0.247, 0.001*	0.167, 0.002*	0.361, 0.274	0.092, 0.193	0.008* , 0.016*	0.371, 0.588	0.523, 0.000*	0.662, 0.418	1.00, 1.00		
10. <i>E. reedi</i>	0.049* , 0.001*	0.153, 0.004*	0.227, 0.819	0.046* , 0.043*	0.006* , 0.878	0.412, 0.005*	0.111, 0.274	0.924, 0.383	0.776, 1.00	1.00, 1.00	
11. <i>P. probus</i>	0.000* , 0.000*	0.317, 0.000*	0.678, 0.799	0.402, 0.047*	0.299, 0.007*	0.185, 0.925	0.041* , 0.000*	0.035* , 0.190	0.089, 0.247	0.101, 0.904	1.00, 1.00

Table 3
A. Descriptive statistics for Orellan ungulate taxa examined in this study. B. Matrices of pairwise probabilities of mean differences in $\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$ values among Orellan ungulate taxa. Values shown in bold indicate significance for $\alpha \leq 0.05$ using Fisher's least significant difference tests. Pairs that were also significant using Tukey's post hoc test are indicated by asterisks (* $\alpha \leq 0.05$).

A. Orellan genus	n	Mean $\delta^{13}\text{C}_\text{E}$ (‰, VPDB)	S.D. (‰)	S.E. (‰)	Range (‰)	Mean $\delta^{18}\text{O}_\text{E}$ (‰, VSMOW)	S.D. (‰)	S.E. (‰)	Range (‰)
<i>Meshippus</i> spp.	8	−8.8	0.5	0.2	−10.6 to −7.9	23.9	1.8	0.6	22.1 to 26.7
<i>Hyracodon nebraskensis</i>	10	−8.9	0.9	0.3	−10.6 to −7.9	25.1	2.9	0.9	20.7 to 28.3
<i>Subhyracodon</i> sp.	4	−9.3	0.8	0.4	−10.2 to −8.3	22.9	1.0	0.5	21.8 to 24.2
<i>Colodon</i> sp.	2	−12.2	0.0	0.0	−12.2	23.4	1.6	1.1	22.3 to 24.5
<i>Archaeotherium mortoni</i>	7	−9.0	1.1	0.4	−11.1 to −7.7	22.3	1.7	0.6	20.1 to 24.5
<i>Agriochoerus antiquus</i>	9	−8.4	0.7	0.2	−9.3 to −7.3	27.0	1.9	0.6	22.5 to 30.0
<i>Merycoidodon</i> sp.	7	−8.9	0.8	0.3	−10.4 to −7.8	22.3	1.1	0.4	21.0 to 23.4
Orellan fauna	47	−8.9	1.1	0.2	−12.2 to −7.3	24.2	2.5	0.4	20.1 to 30.0

B. Orellan $\delta^{13}\text{C}_\text{E}$, $\delta^{18}\text{O}_\text{E}$	1.	2.	3.	4.	5.	6.	7.
1. <i>Meshippus</i> spp.	1.00, 1.00						
2. <i>H. nebraskensis</i>	0.896, 0.339	1.00, 1.00					
3. <i>Subhyracodon</i> sp.	0.233, 0.292	0.486, 0.161	1.00, 1.00				
4. <i>Colodon</i> sp.	0.001* , 0.681	0.001* , 0.433	0.008* , 0.656	1.00, 1.00			
5. <i>A. mortoni</i>	0.580, 0.092	0.717, 0.036*	0.744, 0.569	0.006* , 0.461	1.00, 1.00		
6. <i>A. antiquus</i>	0.217, 0.004*	0.303, 0.108	0.086, 0.002*	0.000* , 0.034*	0.196, 0.000*	1.00, 1.00	
7. <i>Merycoidodon</i> sp.	0.081, 0.052	0.829, 0.027	0.575, 0.410	0.001* , 0.289	0.869, 0.989	0.193, 0.000*	1.00, 1.00

4.3. Chadronian stable isotope paleoecology

Fig. 4 shows mean $\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$ values for ungulates from the Chadronian. Isotopic values and descriptive statistics are reported in Table 2. The mean $\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$ values for all Chadronian samples are $-9.4 \pm 0.1\text{‰}$ and $23.2 \pm 0.2\text{‰}$ ($n = 67$), respectively. *Meshippus* spp. (*Meshippus bairdi* and *Meshippus grandis* are combined here because they are statistically indistinguishable; $\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$, $p = 0.590$ and $p = 0.712$, respectively, Fisher's LSD) has $\delta^{13}\text{C}_\text{E}$ values ($-8.4 \pm 0.3\text{‰}$, $n = 12$) significantly higher than all other taxa except *Agriochoerus antiquus* ($-8.4 \pm 0.6\text{‰}$, $n = 3$, $p = 0.981$, Fisher's LSD) and *Aepinacodon americanum* ($-8.9 \pm 1.0\text{‰}$, $n = 5$, $p = 0.247$, Fisher's LSD). *Megacerops* sp. has $\delta^{13}\text{C}_\text{E}$ values ($-10.9 \pm 0.7\text{‰}$, $n = 7$) significantly lower than all other taxa except *Subhyracodon* (-9.8‰ , $n = 2$, $p = 0.204$, Fisher's LSD) and *Perchoerus probus* ($-10.3 \pm 1.0\text{‰}$, $n = 6$, $p = 0.299$, Fisher's LSD). *Meshippus* has $\delta^{18}\text{O}_\text{E}$ values ($24.0 \pm 0.5\text{‰}$, $n = 12$) significantly different from all other taxa except *Merycoidodon* sp. ($23.3 \pm 1.7\text{‰}$, $n = 8$, $p = 0.135$, Fisher's LSD). *Agriochoerus* has significantly higher $\delta^{18}\text{O}_\text{E}$ values ($26.1 \pm 0.6\text{‰}$, $n = 3$) relative to all taxa except

Table 4
A. Pairwise probabilities of difference in the $\delta^{13}\text{C}$ values between the whole Chadronian and Orellan faunal samples and possible vegetative biomes. Values in bold indicate significance for $\alpha \leq 0.05$ using Fisher's least significant difference tests. These tests clearly show that both faunas were living in "dry", open canopy habitats; based on phytolith assemblage data we can exclude grassland. B. Pairwise probabilities of difference in the $\delta^{13}\text{C}$ values between *Megacerops* sp., *Perchoerus probus*, *Colodon* sp. and riparian habitat.

A. Biomes	Chadronian fauna	Orellan fauna
"Wet" Ituri rainforest (DRC)	<0.001	<0.001
"Wet" monsoon forest (China)	<0.001	<0.001
"Wet" woodland-savanna (Texas)	<0.001	<0.001
"Dry" woody scrubland (Utah)	0.916	0.219
"Dry" C ₃ grassland (Mongolia)	0.429	0.054
"Dry" woodland savanna (South Africa)	0.871	0.506
"Dry" forest (Hawaii)	0.715	0.083

B. Habitat/taxon	<i>Megacerops</i> sp.	<i>P. probus</i>	<i>Colodon</i> sp.
Riparian (open canopy)	0.853	0.424	0.129

Merycoidodon sp. ($23.3 \pm 1.7\text{‰}$, $n = 8$, $p = 0.098$, Fisher's LSD) and *Hyracodon nebraskensis* ($25.2 \pm 1.1\text{‰}$, $n = 7$, $p = 0.325$, Fisher's LSD). *Archaeotherium mortoni* has low $\delta^{18}\text{O}_\text{E}$ values ($21.9 \pm 1.4\text{‰}$, $n = 6$), indistinguishable from all other taxa except *Meshippus*, *Hyracodon*, and *Agriochoerus* ($p = 0.003$, 0.003 , and 0.005 , respectively, Fisher's LSD).

Comparison of our isotopic results with those reported by Zanazzi and Kohn (2008) from the Toadstool area shows that most taxa are not significantly different (Table 5). However, $\delta^{13}\text{C}_\text{E}$ values for both *Meshippus* sp. and *Merycoidodon* sp. are significantly more negative in the Zanazzi and Kohn dataset (Table 5).

4.4. Orellan stable isotope paleoecology

Mean $\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$ values for Orellan ungulates are shown in Fig. 4. Table 3 reports isotopic values and descriptive statistics. The mean $\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$ values for all Orellan samples are $-8.9 \pm 0.2\text{‰}$ and $24.2 \pm 0.4\text{‰}$ ($n = 47$), respectively. As with the Chadronian sample, *Meshippus grandis* and *M. bairdi* are combined in *Meshippus* spp. because they are statistically indistinguishable ($\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$, $p = 0.640$ and $p = 0.989$, respectively, Fisher's LSD). *Colodon* sp. has a significantly lower mean $\delta^{13}\text{C}_\text{E}$ (-12.2‰ , $n = 2$) value compared to the other taxa sampled, but differs in mean $\delta^{18}\text{O}_\text{E}$ values only from *Agriochoerus antiquus*. The other six taxa examined have statistically indistinguishable $\delta^{13}\text{C}_\text{E}$ values. *A. antiquus* ($27.0 \pm 1.3\text{‰}$, $n = 9$) has $\delta^{18}\text{O}_\text{E}$ values significantly higher than all taxa except *Hyracodon nebraskensis* ($25.1 \pm 0.9\text{‰}$, $n = 10$, $p = 0.108$, Fisher's LSD).

Comparison of our isotopic results with those of Zanazzi and Kohn (2008) from the Toadstool area shows that taxa are not significantly different (Table 5).

4.5. Aridity proxies

The aridity index (Levin et al., 2006) yields an estimated increase in water deficit of 90 ± 465 mm/yr (95% confidence) in the Orellan, based on mean $\delta^{18}\text{O}_\text{E}$ values for *Archaeotherium mortoni* (EI) and *Agriochoerus antiquus* (ES). Removing the negative outlier (mentioned above) from the Orellan dataset yields an increase of 204 ± 413 mm/yr. In both cases, propagated error is much greater than the estimated increase

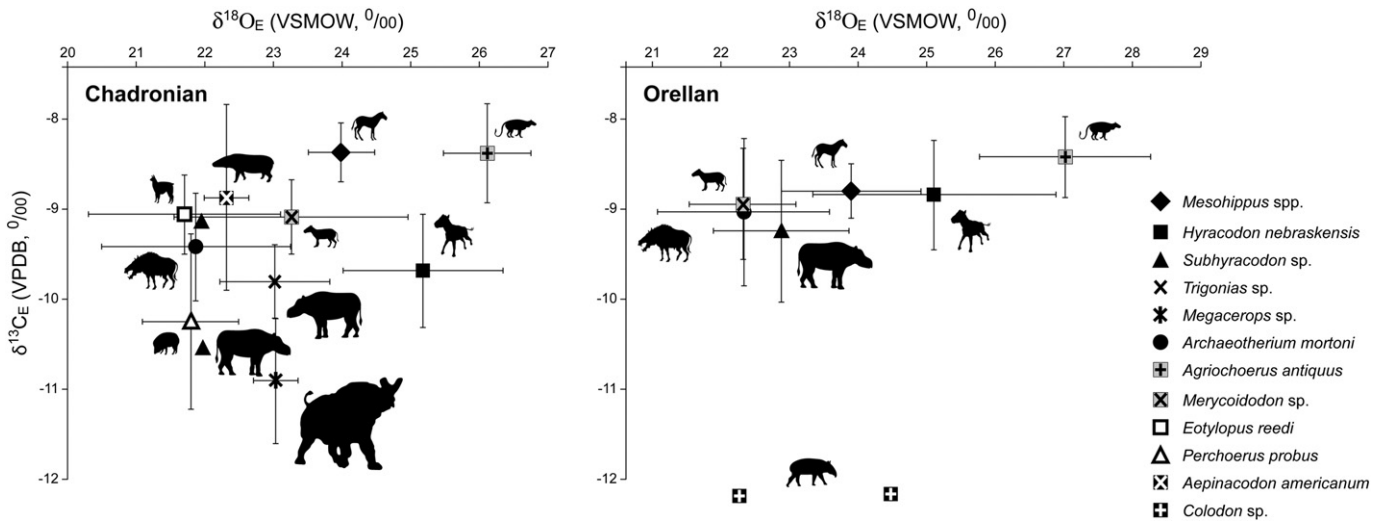


Fig. 4. Scatter plot of $\delta^{13}\text{C}_e$ and $\delta^{18}\text{O}_e$ mean values for Chadronian and Orellan faunas. Error bars show 95% confidence of mean ($\pm 1.96 \cdot \text{SE}$) for taxa with > 2 samples. Solid triangles without bars are individual samples.

in water deficit, making this approach untenable. Taking a different approach, adapting the equation of Kohn (1996, #24) for Dik-diks, an extant aridity-sensitive species (Levin et al., 2006), the 0.9‰ increase in $\delta^{18}\text{O}_e$ values in *A. antiquus* suggests a decrease in relative humidity of $-7 \pm 9\%$ (95% confidence; $1.96 \cdot \text{SE}$), but uncertainty is larger than estimated change. Without the Orellan outlier a greater increase of $11 \pm 7\%$ with lower error is implied. However, these estimates do not take into consideration possible changes in the composition of precipitation unrelated to changes in humidity. Only a small, insignificant change (-0.1% , $p = 0.833$, Fisher's LSD) occurs from the Chadronian to the Orellan in the $\delta^{18}\text{O}_e$ values of all presumed aridity-insensitive taxa (*A. mortoni*, *Merycoidodon* sp., *Subhyracodon* sp.) averaged together, suggesting no change in meteoric water values. However, because of high uncertainty due to high $\delta^{18}\text{O}_e$ variability, a firm conclusion cannot be made using these aridity proxies.

5. Discussion

5.1. Biome and habitat interpretations in the White River Group

All taxa included in this study have $\delta^{13}\text{C}_e$ values consistent with a diet of C_3 vegetation, as expected from previous, pre-latest Miocene isotopic studies. However, some individuals appear to have been feeding in highly water stressed habitats and are approaching the upper range predicted for C_3 vegetation (C_3 -mixed C_3/C_4 boundary $\sim -6\%$). Both the Chadronian and Orellan faunas have mean values

statistically indistinguishable from those predicted for open canopied biomes receiving ≤ 500 mm annual precipitation, such as “dry” woodland-savanna or woody scrubland, and significantly higher than “wet” open or closed canopied biomes receiving ≥ 800 mm of annual precipitation (Fig. 3, Table 4A). Although our mean faunal values are also consistent with C_3 grasslands (Table 4), Strömberg (2004, 2005) found only a small percentage of grass phytoliths in our study area, and it is unlikely that a treeless grassland biome was present. The brontothere *Megacerops* sp. and the peccary *Perchoerus probus* have relatively low mean $\delta^{13}\text{C}_e$ values, statistically indistinguishable from riparian habitat (Fig. 4, Table 4B). It seems unlikely that in a dry woodland-savanna or scrubland biome, any habitat other than riparian would have been extensive enough to support the common *Megacerops* sp., which probably had a large home range (see below). *P. probus*, with its much smaller size (~ 35 kg) and rarity, could conceivably have fed in poorly represented habitats not included in our model, such as areas around springs or ponds that should have similar $\delta^{13}\text{C}_e$ values to riparian habitat. Mean carbon values in the rhinoceroses *Trigonias* sp. (-9.8%) and *Hyracodon nebraskensis* (-9.7%) are slightly below the Chadronian mean (-9.4%) but are not low enough to be confidently assigned to a riparian habitat ($p = 0.029$ and $p = 0.047$, respectively, Fisher's LSD). However, some individuals of these taxa, and of the entelodont *Archaeotherium mortoni*, have low enough values to suggest feeding in riparian areas.

The horse *Meshippus* spp. and the clawed oreodont *Agriochoerus antiquus* have the highest mean $\delta^{13}\text{C}_e$ values ($\sim -8.4\%$) of the Chadronian and Orellan, suggesting that they were feeding in open areas. Other species (*Subhyracodon* sp., *Eotylus reedi*, *Merycoidodon* sp., and *Aepinacodon americanum*) have intermediate $\delta^{13}\text{C}_e$ values, implying that they were feeding on leaves and grasses in more densely vegetated areas than *Meshippus* spp. or *A. antiquus*. Significant differences in mean $\delta^{13}\text{C}_e$ values between our Chadronian samples of *Meshippus* spp. and *Merycoidodon* sp., and those of Zanazzi and Kohn (2008), suggest that these taxa (which could possibly include different species) were feeding in more densely vegetated areas in the populations sampled by Zanazzi and Kohn.

The tapir *Colodon* sp. has the lowest mean $\delta^{13}\text{C}_e$ value (-12.2%) in the Orellan fauna, and is well separated from other taxa (Fig. 4). Its mean value is also lower than any in the Chadronian fauna, although single individuals of *Megacerops* sp. and *Perchoerus probus* are as low. The low values in *Colodon* undoubtedly represent feeding on leaves in or near water. These values are statistically indistinguishable from riparian habitat (Table 4B) although *Colodon* was rare in the WRG and

Table 5

Statistics for Chadronian and Orellan taxa from the Toadstool Park area reported in Zanazzi and Kohn (2008). Differences (Δ) indicate whether the Zanazzi and Kohn (2008) means are more positive or more negative than means from our study. p-Values shown in bold indicate significance for $\alpha \leq 0.05$ using Fisher's least significant difference tests.

	n	$\delta^{13}\text{C}_e$	$\Delta\delta^{13}\text{C}_e$	p	$\delta^{18}\text{O}_e$	$\Delta\delta^{18}\text{O}_e$	p
Chadronian							
<i>Meshippus</i> sp.	7	-9.8	-1.4	<0.001	24.3	0.3	0.520
<i>Subhyracodon</i> sp.	2	-10.1	-0.3	0.822	23.0	1.1	0.143
<i>Megacerops</i> sp.	3	-11.1	-0.2	0.807	22.9	-0.1	0.780
<i>Merycoidodon</i> sp.	6	-10.1	-1.0	0.039	23.2	-0.1	0.948
Orellan							
<i>Meshippus</i> sp.	8	-9E.3	-0.5	0.128	23.2	-0.7	0.378
<i>Subhyracodon</i> sp.	2	-8.8	0.5	0.517	24.7	1.8	0.125
<i>Merycoidodon</i> sp.	7	-9.6	-0.6	0.213	23.3	1.0	0.247

could have fed on vegetation in more restricted habitats, such as around springs or ponds. This is especially interesting because it suggests that *Colodon* occupied a similar ecological niche to Neogene and modern tapirs, which also yield very low $\delta^{13}\text{C}_\text{E}$ values (DeSantis and MacFadden, 2007; DeSantis, 2011). *Colodon* sp. appears to have been morphologically more comparable to extant *Tapirus* (Colbert, 2005) than to earlier forms. Early Eocene tapiromorphs, which were morphologically more generalized, inhabited a wider range of habitats, based on stable isotopes (Secord et al., 2008). These carbon data are the earliest evidence of tapirs occupying a position in the ecosystem similar to the one they occupy today.

5.2. Water dependence

The oreodont *Agriocherus antiquus* has significantly higher $\delta^{18}\text{O}_\text{E}$ values than all other taxa, except *Hyracodon nebraskensis*, in both the Chadronian and Orellan faunas (Fig. 4; Tables 2B and 3B). This strongly suggests that it was getting a larger portion of water from leaves than other taxa, and/or that it had developed a drought-tolerant physiology allowing it to go without regular drinking. It is conceivable that some of the elevation in *A. antiquus* values was caused by sampling only third molars. This would mean that *A. antiquus* followed seasonal breeding cycles and that third molars formed when seasonal $\delta^{18}\text{O}_\text{E}$ values were highest. Although this is possible, it would also mean that the teeth sampled of the taxa to which *A. antiquus* is being compared formed during seasons when values were lower, and because *A. antiquus* maintains the same relative position in isotopic space (Fig. 4) in both faunas, that these conditions held in both the Chadronian and Orellan, in spite of other tooth positions being included in some other taxa. Thus, without additional supporting evidence, it is improbable that tooth position alone accounts for the elevated values exhibited in *A. antiquus*.

Hyracodon nebraskensis and *Mesohippus* spp. have the second and third highest mean $\delta^{18}\text{O}_\text{E}$ values in both the Chadronian and Orellan faunas, respectively, with higher variability in *H. nebraskensis* (Fig. 4, Tables 2B and 3B). As noted earlier, *Mesohippus* spp. was cursorial and was probably a browser or mixed feeder (Table 1). Cursoriality in modern mammals is usually associated with feeding in open areas as a defense against predators. Thus, we would expect that *Mesohippus* spp. was feeding on leaves in open areas, which is consistent with its high $\delta^{18}\text{O}_\text{E}$ and $\delta^{13}\text{C}_\text{E}$ values (Fig. 4). It is interesting, however, that *Mesohippus* sp. appears to be feeding in more closed areas in the Chadronian fauna analyzed by Zanazzi and Kohn (2008), as noted above. With regard to potential bias resulting from sampling third molars, Zanazzi and Kohn (2008) serially sampled five M3s each of *Mesohippus* sp. from the Chadronian and Orellan. Six of the individuals showed a decreasing trend in $\delta^{18}\text{O}_\text{E}$ values, while four individuals did not follow this pattern. In all cases except one, bulk sampling of these teeth would have yielded somewhat averaged annual values or seasonal lows (two teeth), rather than seasonal peaks. Thus the elevated $\delta^{18}\text{O}_\text{E}$ values in our *Mesohippus* spp. teeth cannot be reasonably attributed to sampling primarily third molars. Using *Mesohippus* spp. as a baseline for browsing/mixed-feeding in open areas, the significantly higher $\delta^{18}\text{O}_\text{E}$ values in *Agriocherus antiquus* suggest that *A. antiquus* was less dependent on drinking water and had developed physiological adaptations for retaining water.

We interpret species with low $\delta^{18}\text{O}_\text{E}$ values to have been dependent on drinking water, following patterns seen in modern mammals (Bryant and Froelich, 1995; Levin et al., 2006). This includes the rhinocerotids, *Trigonias* sp. and *Subhyracodon* sp., the brontothere *Megacerops* sp., the entelodont *Archaeotherium mortoni*, the oromerycid *Eotylpus reedi*, the peccary *Perchoerus probus*, and the anthracothere *Aepinacodon americanum* (Fig. 4, Tables 2B and 3B). *A. mortoni* and *P. probus* both have bunodont dentitions, suggesting an omnivorous diet, although Dewar (2008) suggested that *P. probus* was a hard-object browser (i.e., frugivorous “seed predator”) in his unpublished thesis. The low $\delta^{18}\text{O}_\text{E}$ values in these taxa are consistent with the expectation

that non-folivores should have low $\delta^{18}\text{O}_\text{E}$ values relative to the rest of the fauna. The oreodont *Merycoidodon* sp. has intermediate values in the Chadronian, but lower relative values in the Orellan (Fig. 4), indicating that it was also water dependent. The significant increase in faunal mean $\delta^{18}\text{O}_\text{E}$ values (+1.0‰) occurs largely because of the extinction of water dependent taxa and from water dependent species that were sampled in the Chadronian but not in the Orellan due to decreased abundance. This suggests that conditions were less favorable for some water-dependent taxa in the Orellan.

5.3. Environmental response to the Eocene–Oligocene climatic transition

Isotopic results suggest reduction in the extent of wetter, denser habitats with increasing aridity during the Eocene–Oligocene climate transition. An isotopic “gap” in mean $\delta^{13}\text{C}_\text{E}$ values, between $\sim -9.5\%$ and -12% , opens in the Orellan, that was previously filled by mean values of five taxa in the Chadronian (*Hyracodon nebraskensis*, *Subhyracodon* sp., *Trigonias* sp., *Megacerops* sp., and *Perchoerus probus*) (Fig. 4, Tables 2 & 3). Low $\delta^{13}\text{C}_\text{E}$ values in these taxa suggest that they were feeding in wetter, denser parts of the ecosystem. As mentioned above, the low $\delta^{13}\text{C}_\text{E}$ values in *Megacerops* sp. and *P. probus* are consistent with feeding in wetter–denser habitats. The extinction of *Megacerops* sp. and a marked decrease in the abundance of *P. probus*, based on the UNSM collections (12 specimens from the Chadronian collection versus 3 specimens from the Orellan collection, where the Orellan collection is roughly three times the size of the Chadronian), suggest reduction in the extent of the wettest parts of the ecosystem in the Orellan. The rare presence of the tapir *Colodon* sp. in the Orellan suggests such habitats were still present, at least transiently. However, with an estimated body mass of ~ 1900 kg (Mendoza et al., 2006), *Megacerops* sp. should have had a much larger individual home range than *Colodon* sp., which had a body mass of only ~ 150 kg. We estimate that their home ranges were 20 km^2 and 1.5 km^2 , respectively, based on body size (Jetz et al., 2004). It is unlikely that *Megacerops* sp. became extinct due to competition with other mammals, since it was by far the largest mammal in the Chadronian, and no new large-bodied taxa appeared in the Orellan (Russell, 1973). Thus, reduction in the extent of its habitat is the most likely cause for its extinction. In regard to the other “gap” fillers, *Trigonias* sp. became extinct in the Orellan, while the mean $\delta^{13}\text{C}_\text{E}$ values for *H. nebraskensis* and *Subhyracodon* sp. increased, although not significantly.

Along with the reduction in taxa inhabiting wetter–denser habitats we also see an increase in mean faunal $\delta^{18}\text{O}_\text{E}$ values that reflects the loss or reduction of water dependent taxa in the Orellan, as noted above. The reduction of water dependent species and those inhabiting wetter habitats, along with an increase in $\delta^{18}\text{O}_\text{E}$ values in the most aridity-sensitive taxon (*Agriocherus antiquus*), is consistent with increased aridity in the Orellan. However, a marked shift to more arid conditions would be expected to elevate $\delta^{18}\text{O}_\text{E}$ values in other taxa presumed to be aridity-sensitive (*Mesohippus* spp. and *H. nebraskensis*) but mean values in these taxa are virtually unchanged (Fig. 4). It is notable, though, that *H. nebraskensis* has the highest $\delta^{18}\text{O}_\text{E}$ variability of any taxon in the Orellan (Table 3A), potentially masking large shifts in either direction. Another important factor is a significant increase in variance (SD increases by 46%; $p = 0.002$, Welch's F-test) in $\delta^{18}\text{O}_\text{E}$ values (Table 3A and B) in the Orellan. This is consistent with a shift to more arid conditions, which would cause increased water stress in plants, creating greater isotopic heterogeneity in the ecosystem. However, because of this high variability, larger samples are needed to adequately constrain changes in range-through taxa, and paleoenvironmental interpretations made from $\delta^{13}\text{C}_\text{E}$ values should be most reliable.

Our findings are not consistent with the 7 to 8 °C decrease in mean annual temperature in the Orellan proposed by Zanazzi et al. (2007, 2009). Such a massive decrease in temperature should result in a large decrease in faunal $\delta^{18}\text{O}_\text{E}$ values, which is seen neither in our dataset nor theirs (Zanazzi et al., 2007, 2009). Their estimated

drop in temperature is driven almost entirely by an increase in the $\delta^{18}\text{O}$ values of diagenetically reset bone carbonate, which they used as a proxy for soil carbonate. Groundwater $\delta^{18}\text{O}$ values may differ from surface water values, however, and could be influenced by soil water evaporation, by differential mixing of surface and ground water, and by tectonically influenced changes in regional groundwater flow (e.g., Evans and Welzenbach, 1998). A 7 °C decrease should result in a decrease of ~4.1‰ in meteoric water values using the modern relationship between $\delta^{18}\text{O}$ values in precipitation and mean annual temperature at mid-latitudes (0.58‰/°C; Dansgaard, 1964; Rozanski et al., 1993). The slope of this relationship could have been different in the Eocene–Oligocene if there had been a lower latitudinal temperature gradient (e.g., Fricke and Wing, 2004) but the change in $\delta^{18}\text{O}_\text{E}$ values would still have been substantial (e.g., a slope of 0.4‰/°C, results in a change of 2.8‰ in precipitation). A decrease of 4.1‰ in precipitation should result in a decrease of ~5.3‰ in mean faunal $\delta^{18}\text{O}_\text{E}$ values in the Orellan, using the $\delta^{18}\text{O}_\text{E}$ /surface water slope of 0.76 from Kohn's (1996) general herbivore equation. Yet our results show an increase of 1.0‰ in mean faunal values. The large decrease expected in meteoric water values could theoretically have been offset by a ~45% decrease in relative humidity, using Kohn's general herbivore equation, but such a shift would represent a change equivalent to going from moist, sub-tropical conditions to those of a desert, and may be unprecedented. One other possibility is that the large negative shift in precipitation values was compensated for by a change in vapor source or a major reorganization of regional drainage resulting in a ~3–4‰ more positive water source in the Orellan. Changes in circulation through the EOCT are unresolved (e.g. Toggweiler and Bjornsson, 2000; Huber and Sloan, 2001; Huber et al., 2004; Hay et al., 2005; Sijp and England, 2005), and although this hypothesis cannot be falsified, it would require special circumstances and appears to be unlikely.

6. Conclusions

The goal of this study was to evaluate possible changes in biomes or habitat preference in WRG ungulates during the EOCT in response to climate change. Average carbon isotope values for both Chadronian and Orellan faunas suggest that they inhabited a fairly dry biome, such as woodland-savanna or woody scrubland. We find that range-through taxa retain approximately the same relative positions in isotopic space (Fig. 4) in both faunas, implying stability in the habitats occupied by these species. However, an isotopic “gap” in mean $\delta^{13}\text{C}_\text{E}$ values, between ~−9.5‰ and −12‰, that was previously filled by five taxon means in the Chadronian opens up in the Orellan. The Chadronian “gap fillers” appear to have been taxa feeding in wetter parts of the ecosystem, suggesting a reduction in wetter habitats in the Orellan. This change to drier conditions does not appear to be the result of local conditions since two of these taxa (*Megacerops* sp. and *Trigonias* sp.) became extinct regionally in the Orellan. *Megacerops* sp. was by far the largest mammal alive in North America in the Chadronian and was abundantly represented. Thus, its extinction appears to represent an important change in ecosystem structure in the Orellan.

The significant increase of 1.0‰ seen in mean faunal $\delta^{18}\text{O}_\text{E}$ values in the Orellan is also consistent with drying, although the expected response of an upward shift in aridity-sensitive taxa yielded mixed results. Of the 1.0‰ increase, about 0.6‰ resulted from taxa that were sampled in the Chadronian but not the Orellan (which is a much larger collection) due to extinction or poor representation in the latter. This suggests that water dependent taxa did not fare as well as less water dependent taxa in the Orellan. The increase in $\delta^{18}\text{O}_\text{E}$ values in *Agriochoerus antiquus*, the most aridity-sensitive species in both of our faunas, is consistent with the expectation for drying, but significant change was not found in *Mesohippus* spp., which also appears to have been an aridity-sensitive taxon. A significant increase in variance in $\delta^{18}\text{O}_\text{E}$ values (Table 3A and B) that occurs in the

Orellan, is also consistent with an increase in aridity, but weakens the utility of using $\delta^{18}\text{O}_\text{E}$ values in range-through taxa to make paleoclimate interpretations. Paleoenvironmental interpretations made from $\delta^{13}\text{C}_\text{E}$ values, which have bearing on paleoclimate, should be more reliable because of lower overall variability.

Few studies have examined isotopic differences among a diversity of mammals in Pre-Miocene ecosystems dominated by C_3 vegetation. This study further demonstrates the utility of using stable isotopes in mammalian tooth enamel to identify ancient biomes and to recognize habitat differences and the effects of climate in Paleogene C_3 dominated ecosystems.

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Appendix A. Supplementary data

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