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A new stable isotope record of Neogene paleoenvironments and mammalian paleoecologies in the western Great Plains during the expansion of C_4 grasslands

Zachary A. Kita *, Ross Secord, Grant S. Boardman [1]

Department of Earth and Atmospheric Sciences, University of Nebraska, Lincoln, 68588, USA

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ABSTRACT

Stable isotopes in horse teeth from the North American Great Plains show that equids began to incorporate C_4 plants in their diets about 6.5 million years ago as C_4 grasslands expanded. However, the ecological response of many other ungulates to this expansion is poorly documented. We use stable carbon isotopes in mammalian tooth enamel to test whether other ungulates adapted by incorporating C_4 vegetation in their diets. The openness of habitats before the expansion of C_4 grasslands is uncertain, with plant phytolith studies suggesting a patchy environment with open-habitat grasses and forest, and pollen and macrofloral studies suggesting more forested habitats. To address this problem we use a model that predicts carbon isotope values for tooth enamel for a variety of environments, based on values in modern plants. Carbon and oxygen isotopes were analyzed in medium to large herbivores from three late Miocene and three Pliocene local faunas comprising a total of 13 and 7 genera, respectively, and 59 and 42 individuals. Results indicate that before the expansion of C_4 grasslands, taxa with high-crowned teeth were consuming predominantly C_3 vegetation. In contrast, by the late Pliocene most taxa studied were consuming a component of C_4 vegetation and only the peccary *Platygonus* sp. had a pure C_3 diet. C_4 consumption increased in the late Pliocene (~3.0 Ma) Big Springs local fauna probably in response to increased C_4 biomass. Most landscapes in the late Miocene of Nebraska were open, such as woodland-savanna or C_3 grassland, although low carbon values from the Pratt Slide local fauna suggest a denser, presumably forested area. This general pattern suggests an expansion of open-habitats no later than 12 Ma (early Clarendonian). Through the Miocene–Pliocene transition there was an overall shift to lower $\delta^{18}O$ enamel values, which parallels the long-term decrease in global mean annual temperature inferred from the marine record. Our results indicate that major changes in the diets of medium and large herbivores broadly corresponded with increased C_4 biomass and cooling climate from the latest Miocene to the late Pliocene.

1. Introduction

Stable carbon isotope ratios from a variety of proxies, including soil carbonates, mammalian tooth enamel, and grass phytoliths document the global expansion of C_4 grasslands in the late Miocene and Pliocene (Passey et al., 2002; Fox and Koch, 2004; Edwards et al., 2010; McInerney et al., 2011; Strömberg, 2011; Strömberg and McInerney, 2011; Fox et al., 2012a). The timing of this expansion varied considerably among the continents. In the North American Great Plains, 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). Major faunal turnover occurred from the late Miocene to the Pliocene in North America (Cerling et al., 1997; Janis et al., 1998, 2000, 2002, 2004) when a rich diversity of broad-leaf browsing species with low-crowned teeth transitioned to a lower diversity fauna with a greater percentage of higher-crowned grazers (Barry, 1995; Janis et al., 2002, 2004). The timing of changes in crown height do not, however, correspond well with the expansion of C_4 grasslands (e.g., Strömberg, 2006) and hypsodonty appears to be more of a function of habitat openness and aridity than of grass consumption (Mendoza and Palmqvist, 2008; Eronen et al., 2009; Strömberg, 2011). Mammalian species diversity in North America during the middle and late Miocene (Barstovian [16.0–12.5 Ma] and Clarendonian [12.5–9.0 Ma], North American land–mammal ages; Tedford et al., 2004) appears to have been relatively stable, followed by a progressive decrease in diversity with a loss of about two-thirds of the mammalian genera by the end of the Pliocene (Janis et al., 2000, 2002, 2004). Several mammalian groups that were previously well represented (e.g., oreodonts, chalicotheres, and rhinoceroses) disappeared from the Great Plains during this interval (Janis et al., 1998).

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* Corresponding author. Tel.: +1 402 472 2663; fax: +1 402 472 4917.
E-mail address: zkita@huskers.unl.edu (Z.A. Kita).

[1] Currently at: Department of Physics, Astronomy, and Geology, Berry College, Mount Berry, Georgia 30149, USA.

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Uncertainty exists about the types of biomes that were present in the Great Plains prior to the expansion of C_4 grasslands (Strömberg, 2011). Macrofloras and pollen records suggest that open, grass-dominated habitats did not spread until the middle to late Miocene (e.g., Thomasson, 1990; Bolick et al., 1995). Phytolith assemblages, however, suggest that open-habitat grasses expanded at the expense of trees and bamboos to form pooid-dominated savanna woodlands in the late Oligocene or early Miocene. Phytoliths suggest a mixture of grassy and wooded patches until the late Miocene when more uniformly open grasslands spread (Strömberg and McInerney, 2011). A trend of increasing hypsodonty in mammals began around 18 Ma but is not well synchronized with either the macrofloral–pollen or phytolith records, lagging the latter by some 4 myr (Strömberg, 2006).

Another factor complicating our understanding of the expansion of open grasslands is the stable carbon isotope record from soil carbonates that suggests the presence of 12–34% C_4 biomass (mean = 20%) through the early and middle Miocene, preceding the latest Miocene to Pleistocene expansion of C_4 grasslands (Fox and Koch, 2004; Fox et al., 2012a). However, Fox et al. (2012a) indicate that soil carbonate $\delta^{13}C$ values of Clarendonian age from Kansas do not necessarily require any C_4 biomass, nor do all of their Hemphillian samples. High individual $\delta^{13}C_E$ values from a horse tooth (*Cormohipparion*) and rhinoceros tooth (*Teleoceras*) from Ashfall Fossil Beds State Historic Park in Nebraska (Tipple and Pagani, 2007), which is early Clarendonian in age (~12 Ma), are the earliest unambiguous records of C_4 consumption by Great Plains mammals. However, because a large number of ungulates were sampled from the Ashfall locality (Clementz et al., 2008), as well as many horses from other Miocene localities (Passey et al., 2002), it appears that if 20% C_4 biomass were present in the late Miocene only a very small percentage of individuals were exploiting it. This is in spite of several mammal species possessing high-crowned teeth by the late Miocene, which should have enabled them to consume tough grasses.

The reconstruction of paleoenvironments and mammalian paleoecology in the Great Plains is critical for understanding how mammals adapted, or failed to adapt, to environmental change in the late Neogene. Cooling climate and expanding C_4 grasslands would have forced many mammalian groups to adapt to new ecological niches or perish. Previous studies found that horses adapted by incorporating C_4 vegetation in their diets (Wang et al., 1994; Passey et al., 2002), but it is not clear how other taxa responded to a changing ecosystem. With the expansion of C_4 grasslands and the opening of habitats, C_3-dominated environments may have become a minor component of the ecosystem. To test if other mammals adapted by incorporating C_4 vegetation in their diets we analyze the stable isotope composition of tooth enamel from a variety of medium- and large-bodied herbivores. Tooth enamel faithfully records the carbon isotope composition of an individual's diet with predictable C^{13}-enrichment (Cerling and Harris, 1999; Passey et al., 2005) and is used widely to recognize C_3, C_4, or mixed C_3/C_4 diets (e.g., DeNiro and Epstein, 1978; Wang et al., 1994; MacFadden and Cerling, 1996; Koch, 1998; Feranec and MacFadden, 2006). We also use stable isotopes to reconstruct late Miocene (late Clarendonian to middle Hemphillian, 9.5–7 Ma, Tedford et al., 2004) biomes to test whether the landscape contained patches of C_3 grassland and/or forest, as suggested by phytolith studies, or if forests were a more dominant component of the ecosystem before the expansion of C_4 grasses.

We address the following questions: (1) Was the late Miocene (Clarendonian and Hemphillian) landscape largely open with a major component of grasslands or were forests an important component? (2) Were late Miocene mammals consuming C_4 vegetation? The null hypothesis we are testing is that *these mammals were consuming only C_3 vegetation*. (3) How did late Miocene mammals partition habitats? (4) Did non-equid ungulates respond to the expansion of C_4 grasslands by adapting to a partial C_4 diet in a similar fashion to equids? (5) Is there a correspondence between faunal $\delta^{18}O_E$ values from the Great Plains and the global temperature record inferred from benthic carbonates, as might be expected if cooling on the Great Plains mirrored cooling of the oceans?

2. Background

2.1. Geologic context

The geographic distribution of fossil localities and associated faunas used in this study and estimates of their geochronologic ages are shown in Fig. 1. Age estimates are based on the assignment of faunas to biochronologic subdivisions of the Clarendonian, Hemphillian, and Blancan (4.9–2.0 Ma, Bell et al., 2002) North American land–mammal ages by Repenning (1987) and Voorhies (1990). Land–mammal ages and their subdivisions are biochronologic units (Lindsay, 2003) usually based on the first appearance of a taxon or taxa (Wood et al., 1941; Woodburne, 1987, 2004). Boundaries are from Woodburne (2004) and Kelly and Secord (2009).

All teeth sampled in this study are from deposits of fluvial or fluviolacustrine origin. Although these deposits vary in their taphonomic histories, they appear to represent a limited range of fluvial floodplain settings in areas of low relief (Passey et al., 2002). Fossils were sampled from six localities: three from the Ogallala Group of late Miocene age and three from the Broadwater Formation of Pliocene age. The Ogallala Group contains the Pratt Slide and North Shore localities of late Clarendonian age, and the Cambridge locality of medial Hemphillian age (Voorhies, 1990; Passey et al., 2002; Tedford et al., 2004). The Broadwater Formation contains the Lisco locality of early Blancan age, the Broadwater locality of medial Blancan age, and the Big Springs locality of early late Blancan age (Repenning, 1987; Passey et al., 2002). Local faunas from these six sites bear the locality names.

2.2. Carbon isotopes in mammals

Mammalian herbivore tooth enamel faithfully reflects the isotopic composition of ingested plants with predicable enrichment (DeNiro and Epstein, 1978; Vogel, 1978; Cerling and Harris, 1999; Passey et al., 2005). Plant carbon ingested by herbivores is incorporated into the mineralized tissues of the animal. The CO_3 component of tooth enamel therefore reflects the carbon isotope composition of the ingested plants. Both metabolism and biomineralization fractionate ingested carbon so that mammalian bioapatites are enriched in ^{13}C relative to the bulk diet (see Section 3.3).

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. Because C_4 plants have higher $\delta^{13}C$ values than C_3 plants (Vogel, 1978; O'Leary, 1988), with nearly non-overlapping ranges, pure C_3 and C_4 consumers will generally have non-overlapping ranges, while mammals with mixed C_3/C_4 diets will have intermediate $\delta^{13}C_E$ values (MacFadden and Cerling, 1996; Cerling et al., 1997, 1998; Koch, 1998; MacFadden et al., 1999a). Plants using the CAM photosynthetic pathway, characteristic of succulents, have values intermediate or partially overlapping with C_3 and C_4 vegetation (O'Leary, 1988; Ehleringer et al., 1991). However, CAM plants are not widespread (Ehleringer et al., 1991) and typically do not constitute a major part of ungulate diets.

The late Miocene faunas used in this study occurred before the expansion of C_4 grasslands and presumably lived in biomes dominated by C_3 vegetation. Isotopic variability among C_3 plants is caused by differences in light intensity, temperature, nutrient availability, and water stress (O'Leary et al., 1992; Koch, 1998). Generally, $\delta^{13}C$ 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 tooth enamel of herbivorous mammals with high $\delta^{13}C_E$ values representing more open, drier habitats and low values more closed,