



Dietary niche stability of equids across the mid-Miocene Climatic Optimum in Oregon, USA



Kaitlin Clare Maguire*

Department of Integrative Biology and Museum of Paleontology, University of California Berkeley, 1101 Valley Life Sciences Building, Berkeley, CA 94720, USA
School of Natural Sciences, University of California Merced, 5200 Lake Road Merced, CA 95343, USA

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ABSTRACT

During the middle Miocene in North America, hypsodont equids became more diverse and more abundant than brachydont equids. This pattern is evident in middle Miocene deposits of Oregon in which the brachydont taxa became extinct while the hypsodont equids flourished. This turnover, associated with morphological tooth differences, is hypothesized to be a result of dietary differences between taxa, with hypsodont species exploiting the increasing grassland landscape and demise of the brachydont species a result of less vegetation suitable for browsers. Here this hypothesis is tested and the dietary niches of four equid genera are examined using stable carbon and oxygen isotopes. Dietary niche partitioning is evident based on $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values and tooth morphology: *Archaeohippus*, a small brachydont equid, had a narrow dietary niche most likely consuming crown leaf vegetation in the clearings of a woodland habitat; *Parahippus* and *Desmatippus*, medium sized brachydont to incipiently hypsodont equids, ate C_3 vegetation in a relatively open environment; and aff. *Acritohippus*, a larger hypsodont equid, had a broad dietary niche eating C_3 grasses in a relatively open environment. The dietary niches of these four genera did not change through time or across the mid-Miocene Climatic Optimum. Local extinction of the browsing genera, especially *Archaeohippus* with its narrow niche breadth, was most likely due to the opening of habitats as C_3 grasses spread after the mid-Miocene Climatic Optimum. There is no evidence of C_4 vegetation in the diet of aff. *Acritohippus* consistent with the idea that C_4 grasses did not invade the Pacific Northwest during the middle Miocene, in contrast to other regions of North America during that time.

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1. Introduction

The late early Miocene and middle Miocene (~18 to 11.5 Ma) were periods of environmental and climatic change in North America associated with mammalian evolutionary changes and faunal turnover (Webb, 1977; Janis, 1993; Janis et al., 2000, 2002, 2004; Barnosky, 2001; Barnosky and Carrasco, 2002; Kohn and Fremd, 2008; Badgley and Finarelli, 2013). Several ungulate clades (e.g., Antilocapridae, Camelidae, Dromomerycidae, Equidae) diversified; average body size increased within many lineages and morphological innovations (e.g., hypsodonty) emerged (Janis, 1993; Honey et al., 1998; Janis et al., 2000, 2004; Barnosky and Carrasco, 2002; Davis, 2007; Prothero and Foss, 2007; Kohn and Fremd, 2008; Kent-Corson et al., 2013). Diversity of browsing ungulates in North America was greatest during the middle Miocene, higher than any other period in the Cenozoic (Janis et al., 2004). Browsers, brachydont ungulates that primarily eat leafy vegetation from trees and shrubs, began to decline by the late Miocene and grazers, hypsodont ungulates

that primarily eat grasses, became the dominant ungulates, as they are today. It was traditionally hypothesized that grazers out-competed browsers, leading to the extinction of many browsing species. However, in the middle Miocene, browsing ungulates coexisted with grazing ungulates across the continent, suggesting that competition alone did not lead to their extinction (Janis et al., 2004). Instead, it is hypothesized that environmental changes such as spreading grasslands and decreased primary productivity associated with decreased atmospheric CO_2 after the mid-Miocene Climatic Optimum (MMCO), increased selective pressures so that browsing ungulates became extinct and grazers survived and diversified (Janis et al., 2000, 2004).

Equids within the subfamily Equinae are a classic example of a clade in which grazers replaced browsers. The subfamily Equinae underwent an adaptive radiation in which at least 19 new species originated (MacFadden and Hulbert, 1988). This diversification was associated with the emergence of characteristics related to grazing such as hypsodonty, complex enamel patterns, increased body size, and postcranial adaptations for cursorial locomotion in open habitats (MacFadden, 1992, 1997). Overall during this time period there was a decrease in browsing equids and an increase in grazing equids (Janis et al., 2000, 2004). Here this trend is examined at a local scale in Miocene deposits of central Oregon, where the equid fauna shifts from browser-dominated to grazer-dominated. Carbon

* School of Natural Sciences, University of California Merced, 5200 Lake Road Merced, CA 95343, USA.

E-mail address: kmaguire@ucmerced.edu.

and oxygen stable isotope analyses are utilized to: 1) differentiate the diets of browsers and grazers, 2) examine changes in their diets through time, and 3) investigate if changes in their dietary niches were correlated with the success of grazing equids and the demise of browsing equids. If environmental changes increased selective pressures so that browsing ungulates became extinct and grazers survived and diversified, it is hypothesized that the dietary niches of browsers were not broad enough to permit effective utilization of the new vegetation types that accompanied environmental change, nor were the dietary niches able to evolve to adapt to the changing environment. Stable carbon isotope analyses have shown that dietary niches of genera can change and vary as the environment (and particularly the vegetation) changes (DeSantis et al., 2009). Given this, the dietary niches of browsing equids are expected to have been narrow and not evolved, leading to their extinction. This hypothesis is tested by examining the dietary niches of four genera of equids represented in early and middle Miocene deposits of Oregon using stable carbon and oxygen isotopes.

2. Background

2.1. Environmental setting

The morphological changes and diversification of equids in North America during the Miocene were associated with environmental and climatic changes. These phenomena were especially evident in the Pacific Northwest (Kohn and Fremd, 2008). The MMCO occurred approximately 17–14 Ma during which global temperatures rose to a mean annual surface temperature around 18 °C, approximately 3 °C higher than today (You et al., 2009). There is dispute as to the cause of the warming and whether it was associated with increased atmospheric CO₂ (Cerling, 1991; Berner, 1998; Pagani et al., 1999a, 1999b), but paleobotanical analyses, data from fossil mammals, and recent climate simulations suggest that CO₂ levels were at 500 ppm compared to the current level of 400 ppm (Janis et al., 2000; Kürschner et al., 2008; You et al., 2009). Shifts in local climate during the MMCO were not uniform across North America (Retallack, 2007). The Pacific Northwest experienced increased temperatures and humidity during the warming event (Retallack, 2007). Other regions also experienced increased temperatures and humidity but to a lesser extent, e.g., the Northern Rockies had a subhumid climate during the middle Miocene (Barnosky and Labar, 1989; Barnosky, 2001; Retallack, 2007). Tectonic activity increased during the Miocene with the development of the basin and range province in the Great Basin and uplift of the Rocky Mountains beginning by 17.5 Ma (Wernicke and Snow, 1998; McMillan et al., 2002). In Oregon, eruptions of the Columbia River Basalts intensified at 17.2 Ma associated with regional extension and eruption of Steens Mountain in southeastern Oregon at 16.6 Ma (Hooper et al., 2002; Camp and Ross, 2004; Lui and Stegman, 2012). In addition, the Yellowstone Hotspot began erupting at about 16 Ma in southeastern Oregon, increasing topographic relief, diversifying the landscape and potentially stimulating mammalian faunal change in its wake (Kent-Corson et al., 2013).

The replacement of browsers by grazers was originally hypothesized to be associated with the onset and spread of grasses that utilize the C₄ photosynthetic pathway. However, later work demonstrated that a switch from a C₃ to a C₄ diet by ungulates occurred much later, at about 7–8 Ma (Wang et al., 1994), and although C₄ grasses existed on the landscape as far back as the early Oligocene, they did not become widespread until the late Miocene (Edwards et al., 2010). Instead, during the early Miocene, more open habitats emerged in the Great Plains and Northern Rockies with the spread of C₃ grasses (Retallack, 1997, 2004; Strömberg, 2005). Prior to this time, habitats were “closed” and consisted of forested vegetation such as woody or herbaceous angiosperms, conifers, and ferns (Strömberg, 2005). However, there is evidence of C₃ grasses earlier in Oregon. During the late Oligocene in Oregon, bunch grasses grew in wooded grassland and sagebrush habitats and in the early Miocene, sod grasses were abundant in wooded

grassland habitats (Retallack, 2004, 2007). The presence of these grasses, along with paleosol evidence and diversification of burrowing mammals (Samuels and Van Valkenburgh, 2009; Calade et al., 2011) suggests that woodlands were already present and more open habitats were spreading substantially earlier than the early Miocene in Oregon.

2.2. Oregon equids

In the early and middle Miocene deposits of central and eastern Oregon, there were three equid morphotypes belonging to four genera that have been consistently recovered from fossil localities. *Archaeohippus* was a small-bodied equid (average upper first molar length (M1) = 10–13 mm) with brachydont molars (MacFadden, 1998). The *Archaeohippus* lineage is a clear example of dwarfism within the seemingly ubiquitous trend of increased body size in Equidae through time (MacFadden, 1992). Although a small browser, it is adapted for cursoriality with reduced lateral metapodials and an elongate proximal phalanx of the third digit (O’Sullivan, 2003). *Archaeohippus* is within the subfamily Anchitheriinae; however, its relationship to other members in this subfamily is currently unknown (MacFadden, 1998). In Oregon, *Archaeohippus* specimens are recovered from 26 to 14.8 Ma (early Arikareean to early Barstovian) in the John Day, Mascall, and Butte Creek Volcanic Sandstone Formations (Fig. 1). Specimens studied for this analysis from the Mascall Formation (early Barstovian; 16.3 to 14.8 Ma) are assigned to *Archaeohippus ultimus*. Specimens from the John Day Formation (Arikareean to Hemingfordian; 26–16.3 Ma) are not assigned to a species (Dingus, 1990; Hunt and Stepleton, 2004). Those from the Warm Springs locality in the John Day Formation are slightly smaller and lower crowned than *A. ultimus* (Dingus, 1990).

The second equid morphotype in the Miocene of Oregon comprised the brachydont medium-sized (M1 = 15–16 mm) genera *Desmatippus* and *Parahippus*. These genera had similar tooth morphologies but represented opposite ends of the spectrum of anchitheriinae equids ancestral to the Equinae lineage. *Desmatippus* molars lack a crochet and have little to no cement. *Parahippus* molars are mesodont to almost hypsodont with “advanced” forms having a crochet (Fig. 1) and cement (MacFadden, 1998). They have reduced lateral metapodials and an elongate phalanx of the third digit. *Desmatippus* is found in the Mascall and Butte Creek Volcanic Sandstone Formations (early Barstovian; 16.3–14.8 Ma) of Oregon and assigned to the species *D. avus*. *Parahippus* is recovered from the John Day and Mascall Formations (early Arikareean to early Barstovian; 26–14.8 Ma), with specimens from the upper units of the John Day Formation (early Hemingfordian; 17.5–18.8 Ma) referred to *P. pawniensis* and *P. aff. leonensis* (Dingus, 1990; Hunt and Stepleton, 2004) and specimens from the Mascall Formation (early Barstovian; 16.3–14.8 Ma) not assigned to a species (Fig. 1). Because *Desmatippus* and *Parahippus* represent end points of a morphological grade, species assignment of individual specimens is difficult and should not be attempted until a thorough reevaluation of the genera is conducted, a project outside the scope of the current study. As confusion regarding identification may be influencing the stratigraphic ranges, the Oregon stratigraphic ranges reported here represent estimates.

The last morphotype examined in this study is a larger-bodied, hypsodont, tridactyl equid with reduced lateral metapodials, in the merychippine grade of equids. The paraphyletic merychippine grade is basal to the Equinae adaptive radiation and part of the early Miocene diversification of the clade. It is an intermediate between the brachydont browsers and the very hypsodont, large bodied cursorial grazers. There are at least two species of merychippines recovered from middle Miocene deposits in Oregon, a larger species and a smaller species (M.O. Woodburne, pers. communication). The type specimen of the larger species has been attributed to *Hippotherium severus* (Cope, 1886), *H. isonesum* (Cope, 1889), *Stylonus isonesus* (Kelly and Lander, 1988), *Merychippus isonesus* (Gidley, 1906), *Merychippus severus*

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