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Paleodietary reconstruction of fossil horses from the Eocene through Pleistocene of North America

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ABSTRACT

Paleodietary trends for North American horses from *Hyracotherium* (early Eocene) through *Equus* (late Pleistocene) were examined using dental microwear analysis. Over 1200 fossil specimens were analyzed for enamel microwear and results were compared to an extensive microwear database of extant ungulates. This study tests the hypothesis that Eocene horses browsed on low abrasion foods whereas Oligocene and later horses had more abrasive diets concomitant with the spread of more open habitats and examines the correlation between the acquisition of hypsodonty and the beginning of grazing. Microwear results indicate that early to middle Eocene species engaged mostly in fruit browsing. In contrast, late Eocene to Oligocene taxa have microwear scratch numbers typical of grazing and mixed-feeding ungulates, but with very fine scratch textures which are unusual in modern C_4 grazers and indicate consumption of relatively low abrasion grasses. An increase in overall dietary abrasion is evident beginning in the early Miocene but members of the Anchitherinae (sensu stricto) engaged in leaf browsing while other forms committed to grazing or alternating between grass and leaves. Anchitherinae (ss) continue to rely on leaves until they became extinct in the late Miocene, while members of the Equinae were either grazing or mixed feeding through the Pleistocene. Dietary abrasion increased further beginning in the late Miocene and continued to increase through the Pleistocene. Most Pleistocene horses were not grazing but rather alternating between grass and leaves or even browsing. Increased pitting of dental enamel and coarser scratch textures in Plio–Pleistocene horses reinforces the idea that increased abrasion may be due to grit encroachment on food items and/or a shift toward coarser grasses than due to a steady increase in the amount of grass consumed.

1. Introduction

1.1. Background

It is well known that the major evolution and diversification of horses (Equidae) took place in North America. Even so, several successive dispersals occurred to the Old World. While the earliest known equids are known from the Eocene (MacFadden, 1992), the Equidae evolved in apparent isolation from the Old World in North America from the middle Eocene to the late Oligocene. The Miocene witnessed at least three distinct dispersal events of horses into the Old World (MacFadden, 1992; Janis, 2007). However, horses were very widespread in North America during the Tertiary where they are the most common medium- to large-sized mammals found at many fossil localities (MacFadden, 1992). Maximum diversity in equids was achieved in the late Miocene (MacFadden, 1992; Hulbert, 1993).

1.2. Equid adaptive trends

The evolutionary history of horses can be divided into a series of general trends (Matthew, 1926; Simpson, 1951; MacFadden and Hulbert, 1988). While specifics about taxonomy are still under debate, it is generally recognized that horses can be divided into three subfamilies: the Eocene “Hyracotherinae,” the late Eocene to Miocene “Anchitherinae,” and the late Oligocene to Recent Equinae (MacFadden, 1992). Evolution from early forms such as *Hyracotherium* to later forms such as *Equus* involved extensive changes in body size, skeletal and dental morphology, locomotion, and presumably diet. Members of the “Hyracotherinae” were relatively small and had a fairly primitive skull morphology (i.e., short face, short diastema) with brachydont molars with the beginning of ridges between the cusps (bunolophodont) and relatively simple,

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non-molariform premolars (i.e., premolars were small and somewhat triangular). While bunodonty is useful for crushing and pulping foods such as fruit, ridges between cusps are useful for shearing vegetation such as leaves. The material properties of foods influences the evolution of such tooth shapes such that foods with relatively low fiber content like fruits do not have much crack resistance. Therefore, teeth designed to break them generally have rounded cusps, whereas, foods with more fiber content are more resistant, and consumers of such vegetation tend to have sharp blades (Lucas, 2004). The teeth of *Hyracotherium* are therefore considered to be "bunolophodont" and this taxon has tooth wear consistent with a folivorous–frugivorous diet (Janis, 1990, 1995, 2007). In addition, *Hyracotherium* had a dorsally convex back, a four-digit manus, and a three-digit pes, and was subunguligrade (MacFadden, 1986).

In the late Eocene and early Oligocene, *Mesohippus* had a slightly larger body size, a straighter back, and a functionally three-digit manus and pes (tridactyl condition). Forms such as *Mesohippus* ("middle horse") represent an intermediate of sorts between the *Hyracotherium*-like horses of the Eocene and more modern looking later horses. *Mesohippus* and its contemporary *Miohippus* developed cursorial adaptations such as more elongated metapodials and tight locking of articular surfaces as well as a more advanced dentition (Prothero and Schoch, 1989). Their teeth had more developed transverse lophs which suggests a more heavy reliance on shearing vegetation rather than crushing as well as a more fibrous diet. There was also complete molarization of the second through fourth premolars (MacFadden, 1992).

In the early Miocene, parahippine- and merychippine-grade species achieved even larger body size (MacFadden, 1986), complete unguligrady, and other cursorial adaptations, although they were still tridactyl. They represent an important milestone in the evolution of horses as it is within these taxa that molars first became more modern in appearance (i.e., relatively high crowned cheek teeth with well-developed cementum between lophs and with cusps positioned in the same basic patterns as seen in modern horses) (Stirton, 1947; Simpson, 1951; MacFadden and Hulbert, 1988; Bernor et al., 1989, 1997; Prothero and Schoch, 1989; Hulbert and MacFadden, 1991; MacFadden, 1992; Spaan et al., 1994).

It was also in the Miocene that much of the reorganization of the equid skull took place (Radinsky, 1983, 1984), such as an increased preorbital region associated primarily with the expansion of the cheek teeth, a complete postorbital bar, and the concomitant inference of an adaptive shift toward a more abrasive diet (Janis, 1976; Radinsky, 1983, 1984) (Fig. 1). The craniodental trends that began in parahippine and merychippine equids led to the genus *Equus*, which includes all extant horses and is believed to have evolved from *Dinohippus* in the Pliocene (MacFadden, 1984; Hulbert, 1989).

1.3. The Great Transformation and the browsing to grazing transition

It is not surprising that the evolution of the horse has often been cited as a classic example of evolution for over a century and a half given the rich fossil record of horses in North America (particularly in the Miocene). However, it is also true that this "classic story" has been historically misrepresented as an example of orthogenesis or progressive evolution. Also, horses have always been important in human history serving important roles in agriculture, commerce, sport, transport and even warfare (Simpson, 1951; Janis, 2007). Horses also have secured a prominent place in prehistory for the subsistence of hominids evidenced by butchered remains (e.g. Blasco et al., 2010) and also as evidenced by the fact that they are often portrayed in cave paintings and prehistoric sculptures and engravings (Guthrie, 2005).

The evolution of horses involved changes in morphology that reflected sequential adaptations to living in tropical forests, temperate woodlands, woodland/savannas, and finally to seasonal, arid grasslands (Janis, 2007). These evolutionary changes (i.e., high-crowned cheek

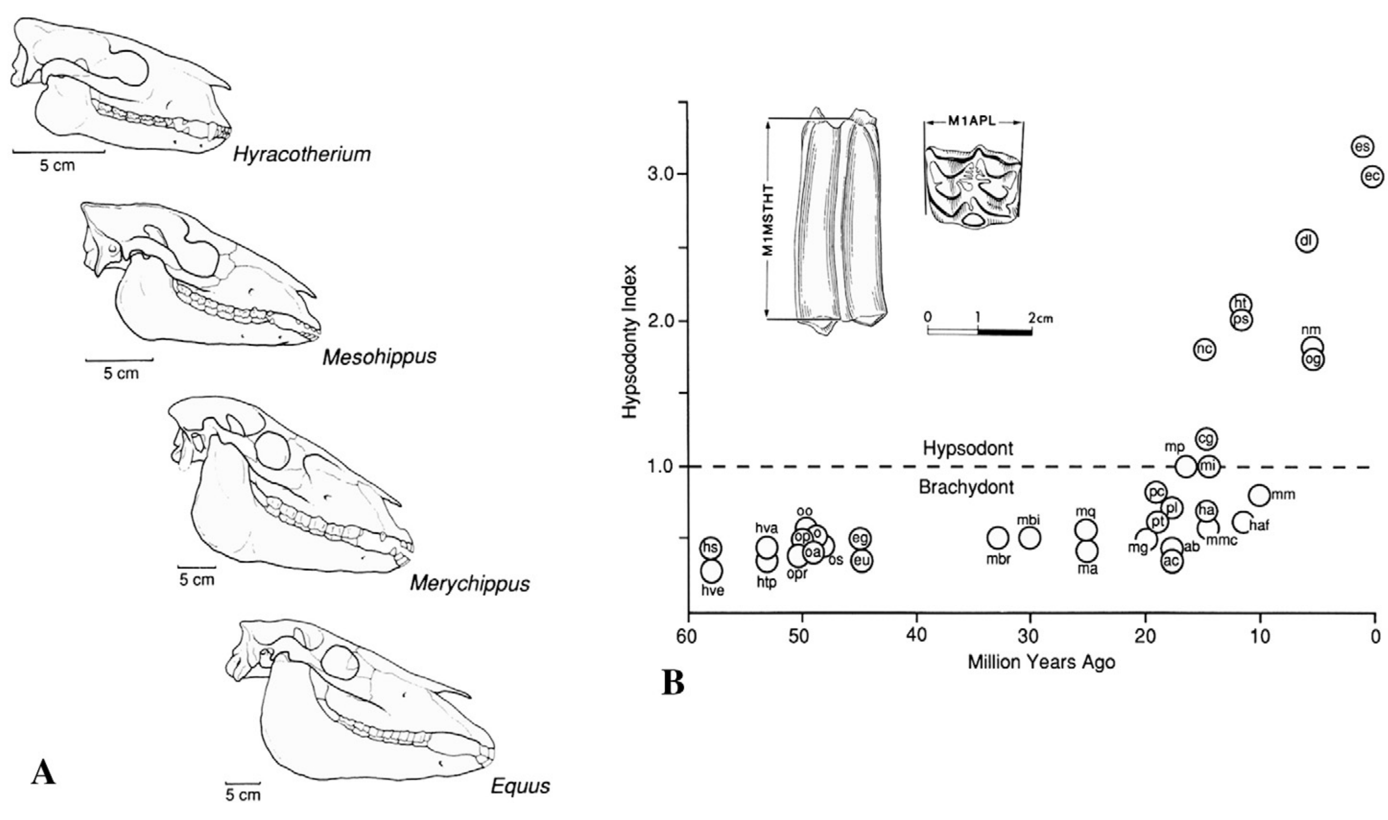

Fig. 1. Reorganization of the equid skull including expansion of the preorbital region and cheek teeth (A) and attainment of hypsodonty and increased complexity of the lophs including well-developed cementum between them first appeared in *Merychippus* ("mi" in B) in the early Miocene (modified from MacFadden, 1992). Key to abbreviations in B as in MacFadden (1992) (Fig. 11.6).