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Trends in the paleodietary habits of fossil camels from the Tertiary and Quaternary of North America

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ABSTRACT

Dietary adaptations of both Tertiary and Quaternary representatives of North American Camelidae were examined through deep evolutionary time (via hypsodonty index), though ecological time (via mesowear analysis), and through the last few days of life (via microwear) by examining molar teeth. Fossil samples are from the Great Plains, Great Basin, Arizona, and Florida and span from the early late Eocene (late Chadronian–early Orellan) to the late Pleistocene (Rancholabrean). Results were compared to those obtained on modern camels and llamas and other ungulates of known dietary behavior. Camels apparently exploited open habitats early on in their evolution as evidenced by the extreme pitting of their enamel surfaces. Grasses were likely consumed early on in their history (e.g., *Poebrotherium*) but the vast majority of taxa were committed browsers. Results show that the hypsodonty pattern (deep time adaptation) and mesowear pattern (cumulative abrasion index) are very similar. Hypsodonty indices and mesowear scores decrease in the middle Miocene, a time when a few taxa also incorporate fruit and/or seeds in their browse. Crown height and dietary abrasion increase in the late Miocene and Pliocene, a time when some grazers and mixed feeders also appear, but then decrease in Pleistocene and Recent forms.

1. Introduction

1.1. Background

The Camelidae includes the camels, guanacos, alpacas, llamas, and vicugnas. The family first appeared in North America in the Uintan (middle Eocene) and was a highly successful group there. Camelids remained endemic to North America until the late Miocene, spending about 36 million years confined there until finally dispersing to Eurasia and Africa in the late Miocene and to South America in the early Pleistocene (Honey et al., 1998). The family experienced their major radiation and diversity in the Miocene of North America where they were found throughout most of the continent. They peaked in diversity during the early and middle Miocene (Hemingfordian and Barstovian) and were often among the most common large herbivores in many fossil faunas over much of North America.

By the end of the middle Miocene (Barstovian), the split between camels and llamas occurred. Camels began to decline during the late Miocene and Pliocene, becoming extinct in North America in the late Pleistocene along with the other North American megafauna (Honey et al., 1998). About 6 million years ago, camels began to spread to other continents. At the end of the last Ice Age, roughly 11,000 years ago, camels and llamas went extinct in North America (i.e., *Palaeolama mirifica*, *Hemiauchenia macrocephala*, and *Camelops hesternus*) (Kurten and Anderson, 1980).

Camels of the Old World and llamas of South America are the living representatives of the suborder Tylopoda, the sister taxon to the Ruminantia within the Neoselonodontia (Webb and Taylor, 1980). In this study, the formal subfamilial divisions of Honey et al. (1998) are followed and the results are reported on representatives of the following subfamilies: Stenomylinae, Protolabinae, Miolabinae, and Camelinae. Samples come from Cenozoic localities in North America which are located principally in four biogeographic regions (following the divisions of Janis et al. (1998): the Northern Great Basin, the Southern Great Basin, the Southern Great Plains, and the Central Great Plains). A few isolated samples were from Florida, and Mexico (Fig. 1).

Camelids, like another endemic North American group, the Antilocaprids, show cursorial adaptations in their limbs from their first appearance (Late Eocene to Early Oligocene) which suggests the early occupation of open habitats (e.g., *Poebrotherium*). Primitive members of the Camelidae were unguligrade, but more advanced forms became digitigrade in their stance. Camels also have elongated necks, some actually becoming giraffe-like (e.g., *Aepycamelus*). By stretching its neck, the modern *Camelus* can browse to a height of 3.5 m (Gauthier-Pilters and Dagg, 1981), thus reaching vegetation in the desert that only climbing goats and giraffes typically can reach. Fossil camels vary in their proportions from sheep or gazelle like to giraffe-like.

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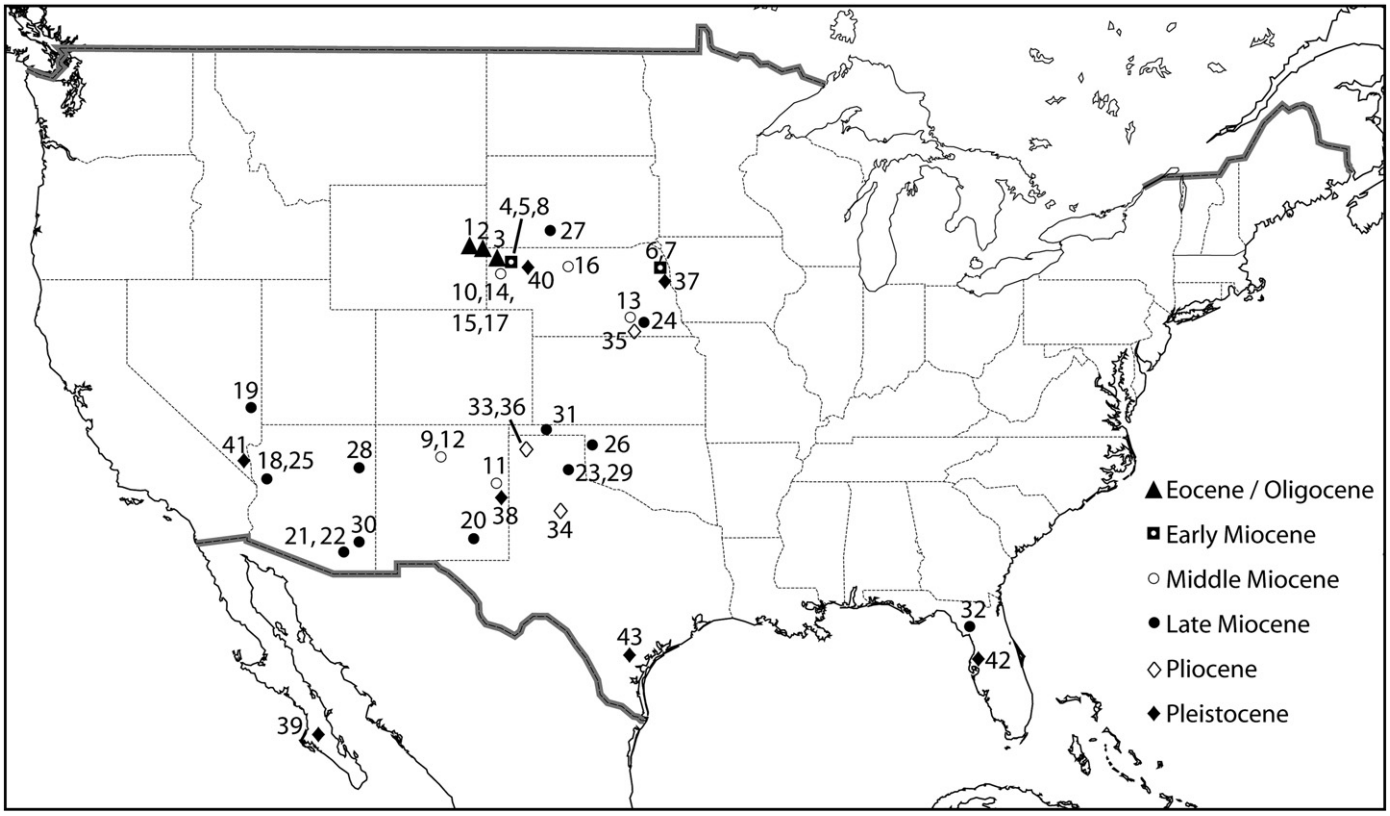

Fig. 1. Location and age of the fossil samples of Camelidae studied. Locality numbers are shown in Table 1.

1.2. Camelid dentition and dietary adaptations

Camelid dentition is primitive among living selenodont artiodactyls in the retention of upper lateral incisors and three premolars. In addition, camels lack the antlers, horns, or ossicones found in many other ungulate groups. However, upper and lower canines are always present and most often caniniform in appearance. Lower incisors are highly spatulate whereas the first two upper incisors are typically reduced or absent in most forms whereas the upper third incisor is present and typically caniniform in appearance (Honey et al., 1998). Cheek teeth span from brachydont to hypsodont.

Modern camels are generally portrayed as intermediate or mixed feeders subsisting on both browse and grass. However, dietary studies on *Camelus* suggest that it is mainly a browser. *Camelus* can consume a significant quantity of grasses (roughly one third of its diet) when necessary however (Gauthier-Pilters, 1984; Newman, 1984; Migongo-Bake and Hansen, 1987; Kohler-Rollefson, 1991; Nowak, 1999). Consequently, it is thought to be a browse dominated mixed feeder, whereas living *Lama* is thought to engage in grass dominated mixed feeding (Puig et al., 1996, 1997; Fraser, 1998, 1999; Nowak, 1999). *Vicugna* incorporates mainly grass in its diet but prizes browse when it is available (Koford, 1957). Therefore, present-day camels are considered to be mixed feeders in open habitats, but they are not necessarily entirely herbivorous, having been observed (e.g., by Gauthier-Pilters, 1984) to eat bones, and even mummified young gazelles.

1.3. Aim of the study

The purpose of this study is to analyze the paleodietary ecology of late Eocene to Recent camelids using three methods of dental wear analysis: (hypsodonty index, mesowear, and microwear). An eclectic array of paleodietary reconstruction tools was used to test the following hypotheses: (1) that camels exploited open habitats early on in their evolution and preferred such habitats throughout their evolutionary history, (2) that increases in crown height in camels are correlated with an increase in grass consumption, (3) that dietary abrasion is concordant with established trends in aridity and temperature in the North American Tertiary and Quaternary. The height of the crown of cheek teeth, also referred to as the level of hypsodonty (Stirton, 1947; Van Valen, 1960; Janis, 1988), has been employed extensively to interpret dietary habits. The greater the level of hypsodonty, the more the functional lifespan of a tooth when confronted with high rates of dental wear (Janis and Fortelius, 1988). Differences in hypsodonty should therefore reflect dietary differences in the processing of plant materials with different physical properties. However, Janis (1988) and Janis et al. (2002) have shown that among extant ungulates, crown height depends upon both diet and the relative openness of the habitat. Thus grazers are generally more hypsodont than browsers and open-habitat forms of all dietary groups are generally more hypsodont than those occupying forested habitats.

Mesowear examines gross wear of molars by examining the shape of cusps in lateral view. This method explores cumulative dental wear imposed on molar teeth during the lifetime of individual animals within taxa. It is a measure of total dietary abrasion incurred in the lifetime of an individual animal including the abrasive elements intrinsic to the plants themselves but also exogenous grit encroaching on food items.

Microwear examines microscopic wear etched into dental enamel presumably via the last meals consumed by these animals just prior to death. Consequently, microwear examines a shorter-term wear such as daily, seasonal, or regional alterations in diet.

Taxa studied via mesowear and microwear and age and locality information for them are shown in Table 1.