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

Gina M. Semprebon [a,*], Florent Rivals [b]

[a] Bay Path College, 588 Longmeadow St., Longmeadow, MA 01106, USA
[b] ICREA and Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Universitat Rovira i Virgili, Avinguda Catalunya 35, 43002 Tarragona, Spain

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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.

* Corresponding author. Fax: +1 413 565 1112.
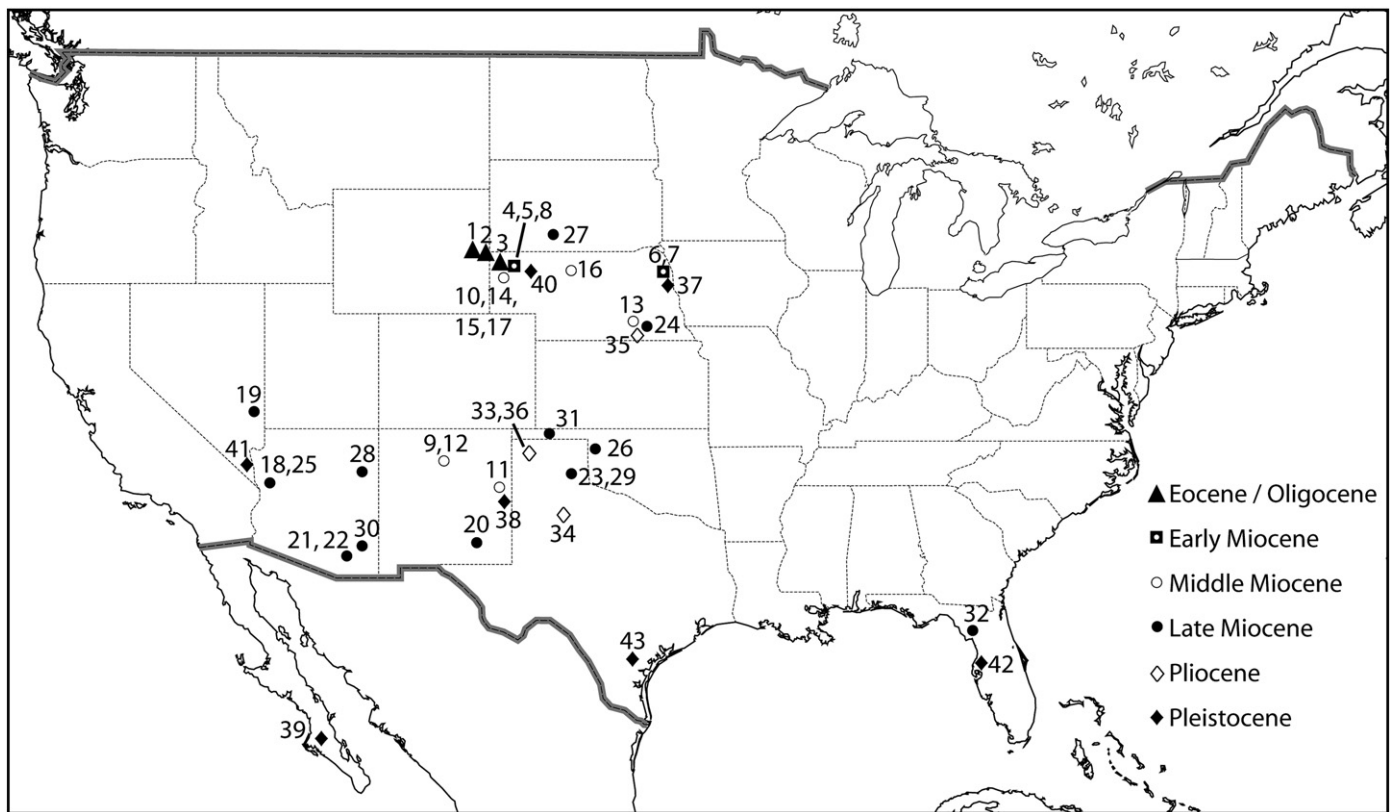E-mail addresses: gsempreb@baypath.edu (G.M. Semprebon), florent.rivals@icrea.es (F. Rivals).

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.

Table 1
Taxa studied for mesowear and microwear analyses.

Sample no. (Fig. 7)	Taxon	Locality	Time
(5)	*Aepycamelus* sp.	Sheep Creek FM, Thompson Qu., Nebraska	Late Hemingfordian
(15)	*Aepycamelus* sp.	Olcott FM, Sioux Co., Nebraska	Early Barstovian
(16)	*Aepycamelus* sp.	Valentine FM, Burge Mbr, Cherry Co., Nebraska	Barstovian/Clarendonian
(16)	*Aepycamelus* sp.	Valentine FM, Crookston's Bridge, Devil's Gulch, and Burge Mbrs., Brown and Cherry Co., Nebraska	Barstovian/Clarendonian
(9)	*Aepycamelus* sp.	Tesuque FM, Pojuaque Mbr, Sante Fe, New Mexico	Barstovian/Clarendonian
(11)	*Aepycamelus proceras*	Olcott FM, Echo Qu., Nebraska	Early Barstovian
(38)	*Camelops* sp.	Clovis Pit, Blackwater Draw, Curry Co., New Mexico	Rancholabrean
(41)	*Camelops nevadanus*	Locality 100, Near Obsidian Artifacts, Clark Co., Nevada	Rancholabrean
(37)	*Camelops* sp.	Hay Springs Area, Dawes, Co., Nebraska	Irvingtonian
(39)	*Camelops* sp.	Comondu Area, Baja California, Mexico	Rancholabrean
(35)	*Gigantocamelus spatula*	Kiem FM, Stegomastodon Qu., Brown Co., Nebraska	Late Blancan
(25)	*Hemiauchenia* sp.	Wikieup Area, Mohave Co., Arizona	Late Hemphillian
(36)	*Hemiauchenia* sp.	Channing Area Hartley Co. Texas	Early Blancan
(32)	*Hemiauchenia* sp.	Alachua FM, Mixson's Bone Bed, Levy Co., Florida	Early Hemphillian
(31)	*Hemiauchenia* sp.	Ogallala FM, Guymon Area, Sandy Clay Flats, Oklahoma	Early Hemphillian
(30)	*Hemiauchenia* sp.	Quiburis FM Old Cabin Qu., Arizona	Late Hemphillian
(40)	*Hemiauchenia macrocephala*	Sheridan FM, Hay Springs Area, Sheridan Co., Nebraska	Late Irvingtonian
(23)	*Machaerocamelus* sp.	Clarendon beds, Donley Co., Texas	Clarendonian
(28)	*Megacamelus* sp.	Keano Canyon, Navajo Co., Arizona	Late Hemphillian
(34)	*Megatylopus* sp.	Mount Blanco, Crosby Co., Texas	Blancan
(18)	*Megatylopus* sp.	Big Sandy FM, Mohave Co., Arizona	Late Hemphillian
(21)	*Megatylopus* sp.	Quiburis FM, Redington Area, Redington Qu., Arizona	Late Hemphillian
(22)	*Megatylopus* sp.	Quiburis FM, Redington Area, Old Cabin Qu., Arizona	Late Hemphillian
(19)	*Megatylopus* sp.	Panaca Area, Lincoln Co., Nevada	Late Hemphillian
(33)	*Megatylopus* sp.	Ogallala FM, Channing Area, Hartley Co., Texas	Early Blancan
(6)	*Michenia* sp.	Runningwater FM, Dunlap Camel Qu., Dawes Co., Nebraska	Early Hemingfordian
(14)	*Miolabis princetonianus*	Olcott FM, Humbug Qu., Sioux Co., Nebraska	Early Barstovian
(42)	*Palaeolama mirifica*	Seminole Field, Melbourne Beds, Florida	Rancholabrean
(43)	*Palaeolama mirifica*	Ingleside, San Patricio Co., Texas	Rancholabrean
(10)	*Paramiolabis singularis*	Olcott FM, Sioux Co., Nebraska	Early Barstovian
(1)	*Poebrotherium* sp.	Douglas, Converse Co., Wyoming	Late Chadronian–early Orellan
(2)	*Poebrotherium* sp.	Lusk, Converse Co., Wyoming	Late Chadronian–early Orellan
(3)	*Poebrotherium wilsoni*	Chadron and Brule FMs, Sioux and Dawes Cos., Nebraska	Orellan
(20)	*Procamelus* sp.	Chamita FM, Thin Elk FM, Round Mtn. Opposite Alcalda River, New Mexico	Early Clarendonian
(27)	*Procamelus* sp.	Thin Elk FM, Ash Hollow FM, Cap Rock Mbr., Little White River, South Dakota	Early Clarendonian
(29)	*Procamelus* sp.	Clarendon beds, Donley Co., Texas	Early Late Clarendonian
(26)	*Procamelus* sp.	Higgins Area, Ellis Co., Oklahoma	Late early Hemphillian
(12)	*Procamelus* sp.	Tesuque FM, New Mexico	Barstovian/Clarendonian
(13)	*Procamelus* sp.	Valentine FM, Brown Co., Nebraska	Barstovian/Clarendonian
(24)	*Procamelus occidentalis*	Ash Hollow FM, Basal Cap Rock Mbr., Brown Co., Nebraska	Early Clarendonian
(7)	*Protolabis* sp.	Runningwater FM, Dunlap Camel Qu., Dawes Co., Nebraska	Early Hemingfordian
(8)	*Protolabis* sp.	Sheep Creek FM, Thompson Qu., Sioux Co., Nebraska	Late Hemingfordian
(17)	*Protolabis* sp.	Olcott FM, Sioux Co., Nebraska	Early Barstovian
(4)	*Stenomylus hitchcocki*	Harrison FM, Galusha Qu., Nebraska	Early late Arikareean

2. Materials and methods

Camel teeth were sampled from the collections of the Division of Paleontology at the American Museum of Natural History (New York) and the Vertebrate Paleontology Laboratory of the University of Texas at Austin (Texas).

2.1. Mesowear analysis

Mesowear analysis (Fortelius and Solounias, 2000) was used to examine attritional (tooth-on-tooth) versus abrasional (food-on-tooth) wear (mesowear) on fossil camelid tooth surfaces. Mesowear has been used extensively recently to gain insight into paleodiet (e.g., Kaiser et al., 2000; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003; Franz-Odendaal and Kaiser, 2003; Semprebon et al., 2004a; Mihlbachler and Solounias, 2006; Rivals and Semprebon, 2006; Semprebon and Rivals (2007a)). In this technique, two variables are assessed: molar cusp shape and occlusal relief in lateral (buccal) view. Only specimens in which the last molar was in occlusion and the first molar retained an occlusal shape similar to that of the second were used in our analysis to minimize age effects on our sample although

the mesowear signal is known to be relatively stable throughout much of the adult lifespan of hypsodont taxa (Rivals et al., 2007a).

As in Fortelius and Solounias (2000), we assessed molar cusp shape by examining the apex of the paracone of the second upper molar and scoring its shape qualitatively as sharp, round, or blunt. We also assessed occlusal relief (the relative difference in height between tooth cusp apices and intercusp valleys) qualitatively as either high or low (i.e., large or small distance between cusp apex and intercusp valley respectively).

Differences in cusp shape and relief are essentially due to relative levels of attrition (sharp cusps and high relief) versus abrasion (more rounded or blunted cusps with lower relief). Individual molar cusp shape and relief scores were converted into a single mesowear score for each fossil taxon to simplify the presentation of data and to ease comparison of various taxa (Rivals and Semprebon, 2006). A combination of sharp cusps with high relief was assigned a score of 0; a combination of rounded cusps with high relief was assigned a score of 1; a combination of rounded cusps with low relief was assigned a score of 2; and a combination of blunt cusps with low relief was assigned a score of 3 (Rivals et al., 2007b). Mesowear scores were then averaged for each individual within a taxon to obtain an average mesowear score for that taxon.

With this scoring system, higher scores represent an increasing dominance of abrasion over attrition, whereas lower scores represent more attritive wear over abrasive wear. The method is not quantitative, no measurement is taken. It is an easy method to compare the samples and assess in a relative way the level of abrasion (more or less abrasion). Therefore, a score close to zero would be found in low abrasion browsers (i.e., mainly high relief and sharp cusp tips). Extreme grazers (high abrasion diet) would typically have blunt cusps and low relief (score of 3), whereas, other dietary groups such as coarse browsers, mixed feeders, and non extreme grazers, would have scores that fall in between these two extreme ends of the continuum.

2.2. Microwear analysis

Microwear features of dental enamel were examined with a light stereomicroscope at 35× magnification following the cleansing, molding, casting, and examination regime developed by Solounias and Semprebon (2002) and Semprebon et al. (2004b). Microwear scars (i.e., rounded pits and elongated scratches) were quantified in a 0.4 mm square area. The average number of pits and average number of scratches was calculated per taxon and results compared to a database constructed from extant ungulate taxa (Solounias and Semprebon, 2002) to determine the dietary categories of browser versus grazer.

It was also noted if more than four large pits were present or absent per microscope field (within the 0.4 mm square area) and whether gouges were present within the 0.4 mm square area. In addition, scratch textures were qualitatively scored as being either predominantly fine, predominantly coarse, a mixture of fine and coarse, or a mixture of coarse and hypercoarse types of textures per tooth surface following the criteria developed to recognize these differences outlined in Solounias and Semprebon (2002) and Semprebon et al. (2004b).

A discriminant analysis was employed to identify the relationship between dietary group assignment and the measured microwear variables. The discriminant models built using extant taxa were then applied to fossil taxon "unknowns" to determine the most probable diet of the various camels studied.

Because extant mixed feeders alternate between browsing and grazing seasonally or regionally, they may overlap the browsing or grazing average scratch/pit morphospaces (Solounias and Semprebon, 2002). For this reason, mixed feeders are also very difficult to classify using discriminant analyses employing average pit and average scratch results. Consequently, to separate out mixed feeders from browsers or grazers, the percentage of scratches in a taxon that fall into a low raw scratch range (i.e., percentage of scratches that fall between 0 and 17) were calculated. Semprebon and Rivals (2007a) have shown that distinctive patterns are seen in extant browsers versus grazers versus mixed feeders when species are sorted this way.

2.3. Hypsodonty analysis

Published hypsodonty data was used on extant ungulates from Janis (1988) and unpublished data provided to us from Christine Janis (Brown University) which reflect a crown height ratio (m3 ratio) obtained as the crown height divided by the labio-lingual width of the lower third molar on unworn teeth. Crown height was taken as the distance from the base of the crown to the tip of the protoconid. Tooth width was measured on the occlusal surface between the outer surfaces of the protoconid and the entoconid. Third lower molar data was chosen because in ungulate taxa such as the extinct stenomyline camelids, this is the only tooth that shows an appreciable degree of hypsodonty. Fossil camel hypsodonty data was then compared to the extant ungulate hypsodonty database. The classification scheme and hypsodonty ranges of Janis (1988) were used when discussing

hypsodonty patterns of fossil camelids as being either brachydont, submesodont, mesodont, or hypsodont.

3. Results

The results of the mesowear analysis (and other analyses) are found in Table 2. The frequencies of each mesowear score expressed as percentages of sharp, round, and blunt cusp shape and high occlusal relief as well as the average mesowear score for each fossil camel taxon are shown. Fig. 2 shows a bivariate plot of mesowear scores (as calculated from data in Fortelius and Solounias, 2000) versus hypsodonty index for extant ungulate browsers; fruit browsers, mixed feeders, and grazers (taxa from Fortelius and Solounias, 2000) and for some fossil camels. The modern dromedary (*Camelus dromedarius*) and vicuna (*Lama vicugna*) are indicated in Fig. 2 by arrows. Fossil camels are identified according to their taxonomic grouping (i.e., subfamily designation).

Fig. 2 shows obvious trends related to diet in terms of mesowear and hypsodonty scores for modern forms. It is apparent that the extant ungulates with the lowest dietary abrasion (i.e., extant leaf-dominated browsers) have the lowest mesowear scores and lowest hypsodonty indices (i.e., are usually brachydont and are attritive feeders), while those with the highest dietary abrasion (i.e., grazers) have relatively high mesowear scores and high hypsodonty indices (i.e., are usually hypsodont and abrasive feeders). There is a significant correlation between hypsodonty and mesowear (Pearson's correlation test; $r = 0.568$; $p = 0.000$). Mixed feeders that browse and graze seasonally or regionally usually have mesowear scores that are intermediate between those of leaf browsers and grazers and are often mesodont. Fruit-dominated browsers have low hypsodonty indices but display higher mesowear scores than leaf-dominated browsers presumably due to the higher abrasiveness of fruit and seed coats versus leaves.

The modern camelids shown in Fig. 2 are fairly hypsodont but both display relatively attritive versus abrasive mesowear scores (low mesowear scores). The modern camelids in Fig. 2 clearly display lower mesowear scores than the fossil forms do regardless of differences in hypsodonty (i.e., *Lama vicugna* is more hypsodont than *Camelus dromedarius* but has a similar mesowear score). This suggests that modern camels have a less abrasive diet than the fossil forms.

Another interesting result is that most of the fossil camels plotted in Fig. 2 have similar mesowear scores regardless of differences in taxonomy (i.e., subfamily designation) and regardless of differences in crown height with the exception of *Stenomylus hitchcocki* which is both very hypsodont and displays a very abrasive mesowear pattern (higher mesowear score = more abrasion).

Fig. 3 shows ungulate hypsodonty patterns and compares extant ungulate hypsodonty patterns with fossil camels. It is apparent in Fig. 3 that there is a great deal of overlap in hypsodonty indices in modern ungulates in different dietary categories. However, browsers (hypsodonty index range = 1.18–2.54) clearly as a rule have lower hypsodonty indices (are more brachydont) than grazers (hypsodonty index range = 3.09–5.83) and most mixed feeders (hypsodonty index range = 1.59–4.89) (especially open-habitat mixed feeders). Also, high-level browsers (open circles) are more brachydont than regular browsers (closed circles) presumably due to less grit exposure. Predictably, grazers have the highest hypsodonty indices and are clearly more hypsodont than browsers as a rule but fresh grass grazers (open circles) are less hypsodont than other grazers (closed circles). Mixed feeders overlap the ranges of browsers and grazers. In particular, mixed feeders in closed habitats (open circles) overlap extensively with browsers.

The present-day camels shown in Fig. 3 have a hypsodonty range [2.25–4.33] comparable to extant mixed feeding bovids and cervids and some fresh grass grazers. The camels overlap fresh grass grazers and mixed feeders while the lamas overlap open-habitat mixed

Table 2

Results of microwear and mesowear analyses. Abbreviations: N = number of specimens; MWS = mesowear score; p = average number of pits; s = average number of scratches; lpp = percentage of individuals per taxon with puncture pits with a diameter of 0.1 mm or larger; mpp = percentage of individuals per taxon with puncture pits with diameters between 0.03 and 0.1 mm; spp = percentage of individuals per taxon with puncture pits with a diameter of 0.03 mm or smaller;%lp = percentage of specimens with large pits;%f = percentage of specimens with fine scratches;%c = percentage of specimens with coarse scratches;%m = percentage of specimens with mixed scratches (fine and coarse);%ch = percentage of specimens with a mix of coarse and hypercoarse scratches;%g = percentage of individuals per taxon with gouges present;%0–17 = percentage of individuals per taxon displaying less than 17 scratches per counting area; B = leaf browser; FB = fruit browser; G = grazer; MF = mixed feeder.

Taxon (sample no. Table 1 and Fig. 7)	Mesowear		Microwear													Probability of group membership
	N	MWS	N	p	s	lpp	mpp	spp	%lp	%f	%c	%m	%ch	%g	%0–17	
Eocene/Oligocene																
Poebrotherium sp. (1)	37	0.78	47	66.8	15.2	0	0	0	100	0	23.4	78.7	0	14.9	70.2 (MF)	1.00 (B)
Poebrotherium sp. (2)	16	0.88	22	61.5	12.3	0	0	0	100	0	40.9	59.1	0	22.7	90.9 (B)	1.00 (B)
Poebrotherium wilsoni (3)	4	1.0	21	78.4	16.4	0	0	0	100	0	47.6	52.4	0	85.7	61.9 (MF)	1.00 (B)
Early Miocene																
Aepycamelus sp. (5)	8	1.5	8	58.4	6.5	0	0	0	100	37.5	0	62.5	0	50	100 (B)	1.00 (B)
Michenia sp. (6)	20	1.1	16	59.2	10.0	0	0	1.2	100	62.5	6.3	33.3	0	25	100 (B)	1.00 (B)
Protolabis sp. (7)	16	1.0	15	65.3	7.4	0	0	0	100	40.0	6.7	53.3	0	33.3	100 (B)	1.00 (B)
Protolabis sp. (8)	8	1.1	7	60.9	6.0	0	0	0	100	28.6	0	71.4	0	57.2	100 (B)	1.00 (B)
Stenomylus hitchcocki (4)	15	2.1	15	76.6	11.4	0	0	0	100	6.6	20	73.3	0	80	93.3 (B)	1.00 (B)
Middle Miocene																
Aepycamelus sp. (16)	8	0.8	9	48.2	11.2	0	0.7	8.3	100	33.4	11.1	22.2	33.3	75	100 (FB)	1.00 (FB)
Aepycamelus sp. (9)	2	1.5	3	50	14.0	0	0.3	10.7	100	33.3	0	0	66.7	66.7	100 (FB)	1.00 (FB)
Aepycamelus proceras (11)	22	1.0	21	35.3	7.6	0	0	0	57.1	66.7	4.7	28.6	0	0	100 (B)	1.00 (B)
Aepycamelus sp. (15)	9	0.9	9	58.6	8.7	0	0	0	100	33.3	0	66.7	0	22.2	100 (B)	1.00 (B)
Miolabis princetonianus (14)	16	0.8	14	53.3	7.1	0	0	0	92.9	7.1	42.9	50	0	35.7	100 (B)	1.00 (B)
Paramiolabis singularis (10)	8	1.1	8	78.8	12.3	0	0	0	100	62.5	0	37.5	0	0	100 (B)	1.00 (B)
Procamelus sp. (12)	12	1.1	11	44.8	17.6	0.3	0.7	12.6	100	0	9.1	27.3	54.6	54.6	45.5 (FB)	1.00 (FB)
Procamelus sp. (13)	23	0.9	28	67.4	17.0	0.1	0	6.4	100	7.1	32.1	39.3	21.4	60.7	50 (FB)	1.00 (B)
Protolabis sp. (17)	7	0.6	8	65.8	8.8	0	0	0	100	62.5	0	37.5	0	37.5	100 (B)	1.00 (B)
Late Miocene																
Hemiauchenia sp. (32)	10	0.9	20	58.1	9.2	0	0.1	3.3	100	60	0	35	5	80	95 (B)	1.00 (B)
Hemiauchenia sp. (30)	46	1.1	46	59.1	9.6	0	0	0	100	34.8	15.2	50	0	47.8	97.8 (B)	1.00 (B)
Hemiauchenia sp. (31)	16	1.1	22	47.7	13.8	0	0	0	90.9	31.8	4.6	54.6	9.1	33.3	59.1 (MF)	1.00 (B)
Hemiauchenia sp. (25)	16	1.4	16	38.6	18.8	0	0	0	93.8	0	62.5	37.5	0	62.5	18.8 (G)	0.59 (B)
Machaerocamelus sp. (23)	67	1.5	73	50.0	12.5	0	0	0	78.1	2.7	9.6	87.7	0	6.9	95.5 (B)	1.00 (B)
Megacamelus sp. (28)	14	1.0	11	68.2	12.1	0	0.2	1.9	100	54.6	9.1	27.3	9.1	63.6	90.9 (FB)	1.00 (B)
Megatylopus sp. (18)	5	2.0	10	31.0	19.9	0	0	0	30	0	10	90	0	10	0 (G)	0.53 (B)
Megatylopus sp. (21)	13	1.5	11	70.8	11.2	0	0	0	100	0	45.5	54.5	0	18.2	90.9 (B)	1.00 (B)
Megatylopus sp. (22)	16	1.6	30	47.9	13.5	0	0	0	100	0	33.3	66.7	0	10	83.3 (B)	1.00 (B)
Megatylopus sp. (19)	3	1.7	5	66.3	9.6	0	0	0	100	0	0	100	0	0	100 (B)	1.00 (B)
Procamelus occidentalis (24)	17	1.4	16	99.4	10.0	0	0	0	100	18.8	12.5	68.8	0	68.7	100 (B)	1.00 (B)
Procamelus sp. (20)	5	1.6	9	70.8	11.3	0	0	3	100	22.2	33.3	44.4	0	44.4	88.9 (B)	1.00 (B)
Procamelus sp. (27)	5	1.2	3	71.7	9.3	0	0	0	100	66.7	0	33.3	0	33.3	100 (B)	1.00 (B)
Procamelus sp. (29)	21	1.2	24	60.1	10.0	0	0.04	1.2	100	16.7	41.7	29.2	12.5	50	95.8 (FB)	1.00 (B)
Procamelus sp. (27)	21	1.3	16	66.3	12.1	0	0	2.3	100	12.5	18.8	62.5	6.3	50	93.8 (B)	1.00 (B)
Pliocene																
Gigantocamelus spatula (35)	1	2	3	53.2	11.7	0	0	0	100	33.3	0	66.7	0	0	100 (B)	1.00 (B)
Hemiauchenia sp. (36)	16	1.4	17	56.5	16.8	0	0	0	100	29.4	11.8	52.9	5.9	11.8	47.1 (MF)	1.00 (B)
Megatylopus sp. (33)	3	2	5	97.7	13.3	0	0	0	100	20	60	20	0	20	100 (B)	1.00 (B)
Megatylopus sp. (34)	5	2	11	57.5	8.2	0	0	0	81.8	54.6	0	27.3	18.2	0	100 (B)	1.00 (B)
Pleistocene																
Camelops sp. (37)	15	2.5	29	69.6	10.6	0	0	0	100	24.1	24.1	48.3	3.5	44.8	96.6 (B)	1.00 (B)
Camelops nevadanus (41)	8	1.1	8	97.6	7.4	0	0	0	0	0	75	25	0	25	100 (B)	1.00 (B)
Camelops sp. (38)	6	1.4	7	54.2	9.0	0	0	0	85.7	0	0	100	0	42.9	100 (B)	1.00 (B)
Camelops sp. (39)	8	1.0	11	66.7	11.7	0	0	0	45.5	27	27	46	0	36.4	90.9 (B)	1.00 (B)
Hemiauchenia macrocephala (40)	15	1.0	16	58.7	18.3	0	0	0	31.3	0	12.5	87.5	0	0	37.5 (MF)	0.99 (B)
Palaeolama mirifica (42)	13	0.8	16	86.4	7.1	0	0	0	50	0	0	100	0	0	100 (B)	1.00 (B)
Palaeolama mirifica (43)	20	0.9	17	66.8	37.3	0	0.2	2.9	82.4	35.3	0	47.1	17.65	11.8	0 (FB)	1.00 (G)
Recent																
Camelus dromedarius (44)	16	0.7	3	54.1	13.9	0	0	0	42.9	42.9	14.3	42.9	0	42.9	71.4 (B)	
Lama vicugna (45)	12	0.6	7	30.4	16.2	0	0	0	57.1	28.6	42.9	28.6	0	85.7	42.9 (MF)	

feeders and grazers. Fossil camels show distinctive patterns. Primitive and relatively early camelids such as *Poebrotherium* fall below this range and have hypsodonty indices that are more like those of browsers or closed-habitat mixed feeders. The more advanced Stenomylinae, Miolabinae, and Protolabinae have hypsodonty indices that fall within the range of present-day open-habitat mixed feeders and fresh grass grazers. Also, it is apparent that the fossil camels that attained the highest hypsodonty levels are the stenomylines and camelines.

Fig. 4 shows camel hypsodonty and mesowear patterns through evolutionary time. Camels are grouped into taxonomic groupings

after Honey et al. (1998). Fig. 4A shows that camels apparently attained more hypsodonty in the early Miocene but crown height was lower in the middle Miocene. There was a trend in the late Miocene toward increased levels of hypsodonty which continued through the Pliocene (no Pleistocene m3 hypsodonty data was available) but was less pronounced into the Recent. Fig. 4B represents a synthesis of both mesowear and microwear patterns in camelids over evolutionary time. Mesowear scores are plotted along a time axis which represents North American Land Mammal Ages. The symbols used to plot the *mesowear* scores indicate the specific dietary assignment given to each taxon from *microwear* analysis (i.e., circles = leaf-dominated
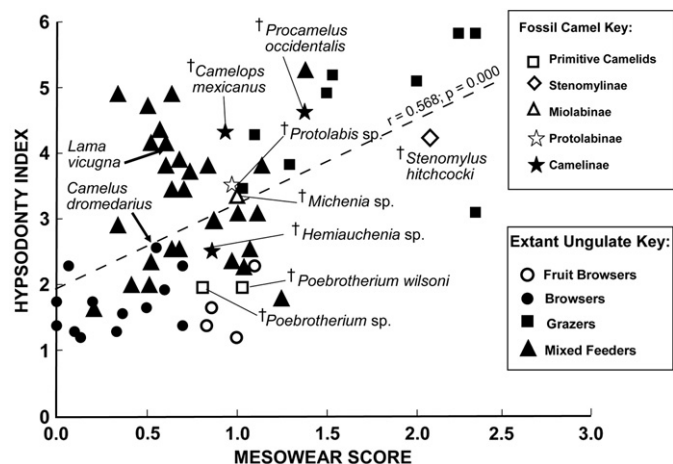
Fig. 2. Bivariate plot of mesowear scores against Hypsodonty Index. Extant data from Fortelius and Solounias (2000). The dashed line represents the regression line ($r = 0.568$; $p = 0.000$) Extant taxa used for this graph: *Cephalophus dorsalis, Cephalophus silvicultor, Dendrohyrax dorsalis, Hyaemoschus aquaticus cottoni, Alces alces, Ammodorcas clarkei, Antilocapra americana, Boocercus euryceros, Capreolus capreolus, Dicerorhinus sumatrensis, Diceros bicornis, Giraffa camelopardalis, Litocranius walleri, Odocoileus hemionus, Odocoileus virginianus, Okapia johnstoni, Rhinoceros sondaicus, Tragelaphus scriptus, Tragelaphus strepsiceros, Aepyceros melampus, Antidorcas marsupialis, Axis porcinus, Boselaphus tragocamelus, Budorcas taxicolor, Camelus dromedarius, Capra ibex, Capricornis sumatraensis, Cervus canadensis, Cervus unicolor, Gazella granti, Gazella thomsoni, Lama vicugna, Ourebia ourebi, Ovibos moschatus, Ovis canadensis, Procavia capensis capensis, Redunca fulvorufula, Rhinoceros unicornis, Saiga tatarica, Syncerus caffer aequinoctialis, Taurotragus oryx, Tetracerus quadricornis, Tragelaphus angasi, Tragelaphus imberbis, Alcelaphus buselaphus, Bison bison, Ceratotherium simum, Connochaetes taurinus, Damaliscus lunatus, Equus burchelli, Equus grevyi, Hippotragus equines, Hippotragus niger, Kobus ellipsiprymnus.*

browsers, stars = regional or seasonal mixed feeders, and squares = grazers). Mesowear is scored on a scale of 0–3 (Materials and methods description) and represents a range of attritive versus abrasive gross

dental wear. This range is due to either predominantly tooth-on-tooth wear (attrition dominates over abrasion resulting in low mesowear scores) as seen when teeth completely cut though soft and "clean" or non-gritty food items or food-on-tooth wear (abrasion dominates over attrition resulting in high mesowear) as seen when abrasive food items wear teeth.

From the late Eocene and Early Oligocene to the early Miocene, there is a rise in abrasion (increasing mesowear scores). However, middle Miocene camelid diets are less abrasive than early Miocene diets. After the middle Miocene, camels apparently shifted to more abrasive diets until the late Pleistocene and then back to more attritive diets in the Recent. It is apparent that no fossil or living camels has mesowear consistent with high abrasion modern grazing (mesowear scores close to 3 indicating low relief and blunting of cusps) such as that employed by modern bison or horses although *Camelops* sp. from the Hay Springs Area of Nebraska shows fairly abrasive mesowear. However, this taxon apparently was a "dirty browser" based on microwear results. Fig. 4B also shows that even when grass was consumed by camels (stars and squares in the chart), the grasses apparently were not highly abrasive in nature.

Microwear results are summarized in Table 2 and Figs. 4B and 5. Fig. 5 shows dietary patterns of microwear seen in extant grazers, browsers, and mixed feeders (after Solounias and Semprebon, 2002). The average number of scratches versus the average number of pits per taxon is shown (at 35× magnification). In Fig. 5A, it is clear that there is no overlap in microwear results between the extant grazing and browsing taxa. However, mixed feeders switch from browse to grass seasonally or regionally and consequently often fall in the gap between grazers and browsers in terms of average number of scratches (Solounias and Semprebon, 2002) (Fig. 5B). Also, mixed feeders may have average scratch values that overlap with those of browsers or grazers depending on whether they typically consume relatively more browse or grass. Because of this, additional calculations are necessary to discriminate them from other trophic groups. Such mixed feeding taxa display bimodal scratch distributions
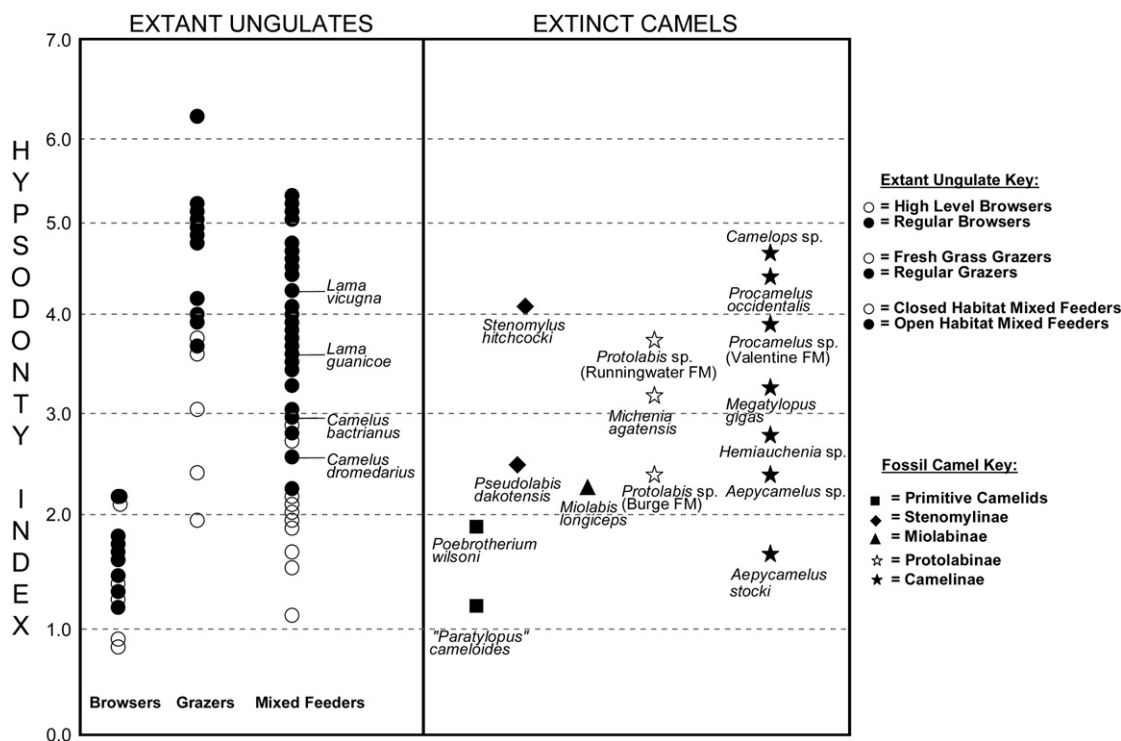

Fig. 3. Extant ungulate and camelid hypsodonty indices. Extant ungulates are represented by circles (closed circles = regular browsers, grazers, and mixed feeders; open circles = high-level browsers, grazers, and mixed feeders). Fossil camelids are separated taxonomically (closed squares = primitive camelids; closed diamonds = Stenomylinae; closed triangles = Miolabinae; open stars = Protolabinae; closed stars = Camelinae).
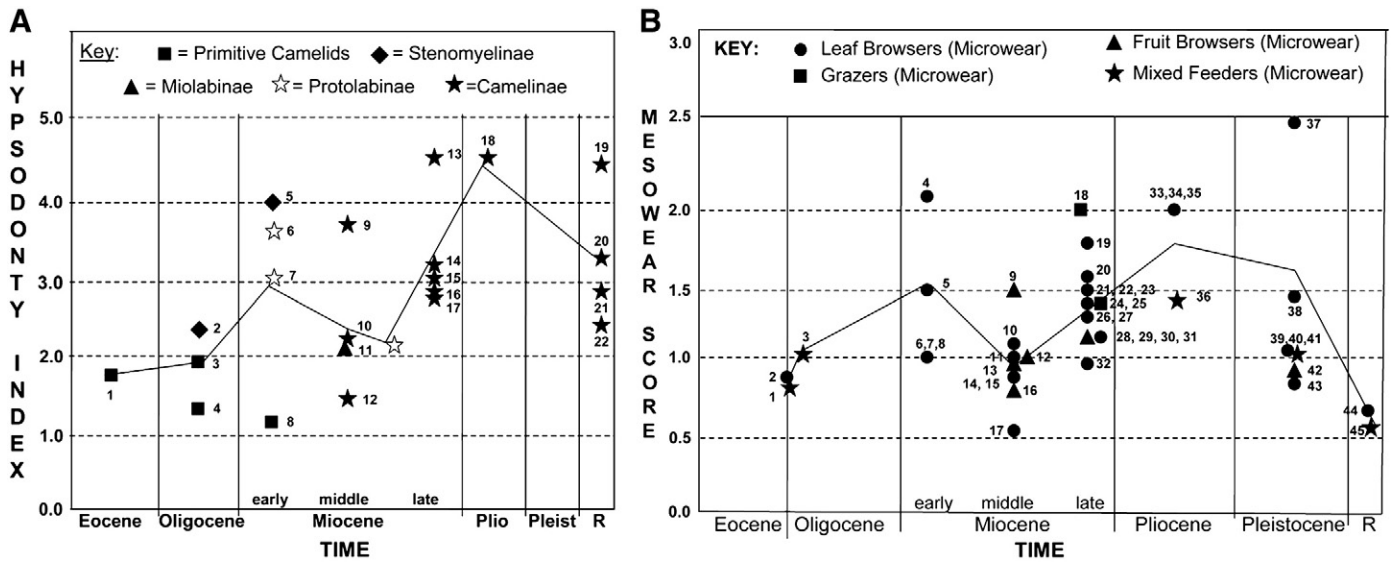
Fig. 4. Camel hypsodonty, mesowear, and microwear patterns through time. A. Key: 1 = *Poebrotherium eximus*, 2 = *Pseudolabis dakotensis*, 3 = *Poebrotherium wilsoni*, 4 = *Poabromylus kayi*, 5 = *Stenomylus hitchcocki*, 6 = *Protolabis* sp. (Runningwater Formation, Nebraska), 7 = *Michenia* sp. (Runningwater Formation, Nebraska), 8 = *Paratylopus cameloides*, 9 = *Procamelus* sp. (Valentine Formation, Nebraska), 10 = *Aepycamelus* sp. (Pawnee Creek Formation), 11 = *Miolabis longiceps*, 12 = *Aepycamelus stocki*, 13 = *Procamelus occidentalis*, 14 = *Megatylopus gigas*, 15 = *Procamelus* sp. (Love Site), 16 = *Hemiauchenia* sp. (Love Site), 17 = *Aepycamelus* sp. (Ash Hollow Formation), 18 = *Camelops mexicanus*, 19 = *Lama vicugna*, 20 = *Lama guanicoe*, 21 = *Camelus bactrianus*, 22 = *Camelus dromedarius*. B. Key: Key: 1 = *Poebrotherium* sp. (Douglas Wyoming), 2 = *Poebrotherium* sp. (Lusk Wyoming), 3 = *Poebrotherium wilsoni* (Chadron and Brule Formations, Nebraska), 4 = *Stenomylus hitchcocki* (Harrison Formation, Nebraska), 5 = *Aepycamelus* sp. (Sheep Creek Formation, Nebraska), 6, 7, 8 = *Michenia* sp. (Runningwater Formation, Nebraska), *Protolabis* sp. (Runningwater Formation, Nebraska), *Protolabis* sp. (Sheep Creek Formation, Nebraska), 9 = *Aepycamelus* sp. (Tesuque Formation, New Mexico), 10 = *Paramiolabis singularis* (Olcott Formation, Nebraska), 11 = *Aepycamelus proceras* (Olcott Formation, Nebraska), 12 = *Procamelus* sp. (Tesuque Formation, New Mexico), 13 = *Procamelus* sp. (Valentine Formation, Nebraska), 14, 15 = *Miolabis princetonianus* (Olcott Formation, Nebraska) and *Aepycamelus* sp. (Olcott Formation, Nebraska), 16 = *Aepycamelus* sp. (Valentine Formation, Nebraska), 17 = *Protolabis* sp. (Olcott Formation, Nebraska), 18 = *Megatylopus* sp. (Big Sandy Formation, Arizona), 19 = *Megatylopus* sp. (Panaca Area, Nevada), 20 = *Procamelus* sp. (Chamita Formation, New Mexico), 21, 22, 23 = *Megatylopus* sp. (Quiburis Formation, Arizona — Redington Quarry), *Megatylopus* sp. (Quiburis Formation, Old Cabin Quarry), *Machaerocamelus* sp. (Clarendon Beds, Texas), 24, 25 = *Procamelus occidentalis* (Ash Hollow Formation, Nebraska) and *Hemiauchenia* sp. (Wikieup Area, Arizona), 26, 27 = *Procamelus* sp. (Higgins Area, Oklahoma) and *Procamelus* sp. (Thin Elk Formation, South Dakota), 28, 29, 30, 31 = *Megacamelus* sp. (Keano Canyon, Arizona), *Procamelus* sp. (Clarendon Beds, Texas), *Hemiauchenia* sp. (Quiburis Formation, Arizona), and *Hemiauchenia* sp. (Ogallala Formation, Oklahoma), 32 = *Hemiauchenia* (Alachua Formation, Florida), 33, 34, 35 = *Megatylopus* sp. (Channing Area, Texas), *Megatylopus* sp. (Mount Blanco, Texas), and *Gigantocamelus spatula* (Kiem Formation, Nebraska), 36 = *Hemiauchenia* sp. (Channing Area, Texas), 37 = *Camelops* sp. (Hay Springs Area, Nebraska), 38 = *Camelops* sp. (Blackwater Draw, New Mexico), 39, 40, 41 = *Camelops* sp. (Comondu Area Baja California/Mexico), *Hemiauchenia macrocephala* (Sheridan Formation, Nebraska), *Camelops nevadanus* (Locality 100, Nevada), 42 = *Palaeolama mirifica* (Melbourne Beds, Florida), 43 = *Palaeolama mirifica* (Ingleside, Texas), 44 = *Camelus dromedarius* (Africa), 45 = *Lama vicugna* (South America).

when individual raw scratch results are graphed (Solounias and Semprebon, 2002).

Good separation may also be attained between extant browsers, grazers, and mixed feeders by calculating the percentage of individuals per taxon possessing scratch numbers between 0 and 17 (i.e., the percentage of scratches per taxon that fall in the low-scratch range). Semprebon and Rivals (2007a) have shown that there is no overlap between the low-scratch ranges of extant leaf-dominated browsers (72.73–100% of scratches fall between 0 and 17) (raw data from Solounias and Semprebon, 2002) and grazers (0–22.2% of scratches fall between 0 and 17). Fortunately, no overlap is seen in the raw scratch ranges of browsers and seasonal or regional mixed feeders and very little overlap is seen between grazers and seasonal or regional mixed feeders (20.93–70% of scratches fall between 0 and 17). Mixed feeders that alternate between browse and grass more frequently than on a seasonal or regional basis (meal-by-meal mixed feeders) are distinctive from seasonal and regional mixed feeders but overlap with the low-scratch ranges of grazers (most likely the more frequent consumption of abrasive grasses by meal-by-meal mixed feeders as opposed to regional or seasonal mixed feeders overrides the less abrasive browsing microwear signature in these latter forms). Table 2 shows low-scratch percentages for the taxa studied here and dietary designations assigned to those taxa based on extant ungulates of known dietary categories (Semprebon and Rivals, 2007a).

Fig. 6 shows results for the fossil camels studied here in relation to results obtained on extant ungulates of known diets. Note in Fig. 6 that fossil camelids (and modern camels in Fig. 5A) display far more pitting

than typically seen in modern ungulates of any trophic category. Fig. 6A shows scratch/pit results for the Eocene and Oligocene fossil camels studied. *Poebrotherium wilsoni* from the Chadron and Brule Formations of Nebraska and *Poebrotherium* sp. from Douglas Wyoming show a pattern similar to modern regional or seasonal mixed feeding ungulates in terms of scratch results. However, as stated before, significantly more pitting is seen in camels than in any extant ungulate studied thus far by microwear analysis. *Poebrotherium* sp. from Lusk Wyoming has results similar to extant browsers (falling very close to results for *Camelus dromedarius*). Fig. 6B–D shows microwear scratch/pit results for Miocene fossil camelids. Early and middle Miocene fossil camels have results concordant with modern browsers although, in the middle Miocene, fruit apparently became incorporated more heavily into the browsing dietary regime, as *Aepycamelus* sp. from both the Tesuque and Valentine Formations of Nebraska and *Procamelus* sp. from the same formations and states show the puncture-like large pit results (Table 2 and Fig. 7) seen in extant fruit browsers (Solounias and Semprebon (2002) and Semprebon et al. (2004b) for more details on fruit browsing microwear patterns). It is not until the late Miocene (Fig. 6F) that a shift toward mixed feeding (*Hemiauchenia* sp. from the Ogallala Formation of Oklahoma) and grazing (*Hemiauchenia* sp. from the Wikieup Area of Arizona and *Megatylopus* sp. from the Big Sandy Formation of Arizona) is seen. Note however, that the majority of fossil camels are browsing in the late Miocene and *Megacamelus* sp. from Keano Canyon in Arizona has results consistent with some fruit browsing (e.g., puncture pit results in Table 2).
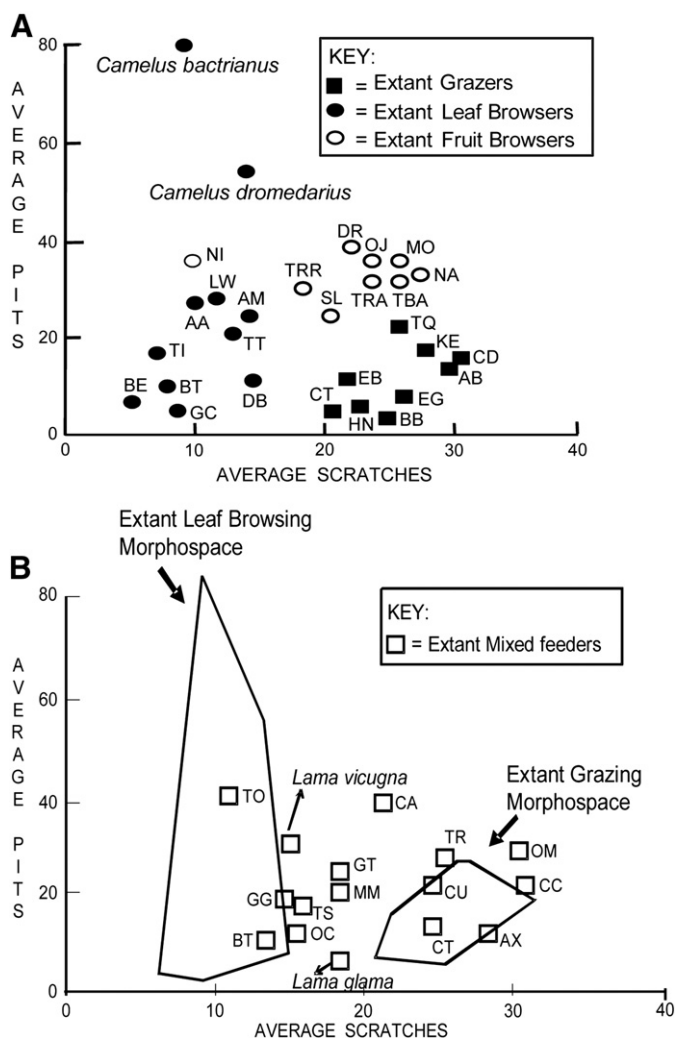
Fig. 5. Bivariate plot of the average number of pits versus average number of scratches in extant ungulates. Microwear obtained at 35× magnification with a stereomicroscope (extant data from Solounias and Semprebon, 2002). Convex hulls are drawn around extant leaf browsing taxa and extant grazing taxa for ease of comparison. A, plot of the average number of pits versus the average number of scratches of extant leaf-dominated browsers, extant grazers, and extant fruit-dominated browsers. B, plot of the average number of pits versus the average number of scratches for extant ungulate mixed feeders. Abbreviations for (A): Leaf browsers: AA, *Alces alces*; AM, *Antilocapra americana*; BE, *Tragelaphus eurycerus*; CB, *Camelus bactrianus*; CL, *Camelus dromedarius*; DB, *Diceros bicornis*; GC, *Giraffa camelopardalis*; LW, *Litocranius walleri*; TI, *Tragelaphus imberbis*; TT, *Tragelaphus strepsiceros*. Fruit browsers: DR, *Cephalophus dorsalis*; MO, *Moschus moschiferus*; NA, *Cephalophus natalensis*; NI, *Cephalophus niger*; OJ, *Okapia johnstoni*; SL, *Cephalophus silvicultor*; TBA, *Tapirus bairdii*; TRA, *Tragulus spp.*; TRR, *Tapirus terrestris*. Grazers: AB, *Alcelaphus buselaphus*; BB, *Bison bison*; CD, *Cervus duvauceli*; CT, *Connochaetes taurinus*; EB, *Equus burchelli*; EG, *Equus grevyi*; HN, *Hippotragus niger*; KE, *Kobus ellipsiprymnus*; TQ, *Tetracercus quadricornis*. Abbreviations for (B): AX, *Axis axis*, BT, *Budorcas taxicolor*, CA, *Capricornis sumatraensis*, CC, *Cervus canadensis*, CI, *Capra ibex*, CU, *Cervus unicolor*, GG, *Gazella granti*, GT, *Gazella thomsoni*, LG, *Lama glama*, MM, *Muntiacus muntjak*, OC, *Ovis canadensis*, OM, *Ovibos moschatus*, TO, *Taurotragus oryx*, TR, *Boselaphus tragocamelus*, TS, *Tragelaphus scriptus*, VI, *Lama vicugna*.

Fig. 6G and F shows Pliocene and Pleistocene camel scratch/pit results respectively. The Pliocene and Pleistocene camels apparently mainly browsed with a few forms engaging in mixed feeding (*Hemiauchenia* sp. from Channing Area of Texas and *Hemiauchenia macrocephala* from the Sheridan Formation of Nebraska). *Palaeolama mirifica* from Ingleside in Texas has interesting results with some individuals displaying puncture-like large pits typical of some fruit consumption (Table 2).

Table 2 and Fig. 7 depict the results of the discriminant analyses. The microwear variables that built the most accurate model were the

average number of pits, average number of scratches, average number of small puncture pits, average number of medium puncture pits, and average number of large puncture pits and large pits. Fig. 7 shows the association between predicted and actual dietary group membership for extant taxa as is reflected by the percentages of correct classifications within each trophic category as shown. These percentages represent the accuracy of the model built using extant taxa with known diets in predicting the actual trophic group membership of these taxa (data from Solounias and Semprebon, 2002 and Semprebon, 2002). Fig. 7A represents the discrimination of extant taxa with known diets when canonical scores are plotted for the three canonical variables (i.e., those variables that capture most of the differences between extant dietary groups). Based on their values for the six microwear variables that were used to build the discriminant model (described above), extant taxa were assigned to one of four dietary groups (leaf browser, fruit browser, grazer, or mixed feeder). Fig. 7A shows that the six microwear variables described above are highly effective in discriminating between extant leaf browsers (82% accurate), fruit browsers (88% accurate) and grazers (78% accurate). As expected, mixed feeders that alternate between browse and grass regionally or seasonally cannot be readily distinguished from the other trophic groups (40% accurate) as discussed above. Consequently, extant mixed feeders were eliminated from the analysis shown in Fig. 7B and mixed feeders were identified using the low-scratch method (i.e., % of scratches per individual that fall between 0 and 17) described above. Fossil camel taxa were inserted as unknowns into this second discriminant model (Fig. 7B) and the most probable diet for each taxon determined and shown via probability of trophic group membership in Table 2.

Fig. 8 shows examples of enamel scar patterns on the dental enamel of some of the fossil camels studied here. The vast majority of camel taxa that we studied have browsing microwear scar patterns as seen in Fig. 7A (*Machaerocamelus* sp. from the Clarendon Beds of Texas) and B (*Megatylopus* sp. from the Quiburis FM, Old Cabin Quarry, Arizona). That is, very few scratches are visible. However, as previously stated, both extant and fossil camel enamel is more heavily pitted than that of other extant ungulates and often displays gouges along the enamel band edges as is seen in Fig. 7A and B. Fig. 7C shows a more scratched surface typical of grass consumption which is found in only a few camel taxa studied here (Table 3 for average scratch counts per taxon and dietary categorizations) such as *Poebrotherium wilsoni* from the Chadron and Brule Formations of Nebraska. Fig. 7D shows the unusually large and deep puncture-like pits characteristic of extant fruit browsers in *Aepyceros* sp. from the Valentine FM, Burge Member, Nebraska.

Fig. 9 shows a hypothesis of camelid relationships following Honey et al. (1998) with a dietary assignation given to taxa based on the results of this study. It is clear in Fig. 9 that there is no obvious dietary pattern related to phylogeny.

4. Discussion

4.1. Primitive camelids

Table 3 represents a synthesis and summary of the results of this study and those of others pertinent to the dietary reconstruction of the fossil camels studied and discussed here. Results on the primitive camelids in our database are interesting for several reasons. Firstly, they show that a primitive representative of a family may be a grass consumer rather than displaying the pure browsing diet typical of many early representatives of ungulate families. Secondly, our results reveal that a particular taxon may exhibit different diets in different localities, even those relatively near one another (e.g., *Poebrotherium* sp. from Lusk Wyoming versus *Poebrotherium* sp. from Douglas Wyoming). Thirdly, the very high pit counts found on *Poebrotherium* enamel and all of the fossil camels studied indicate that camels have
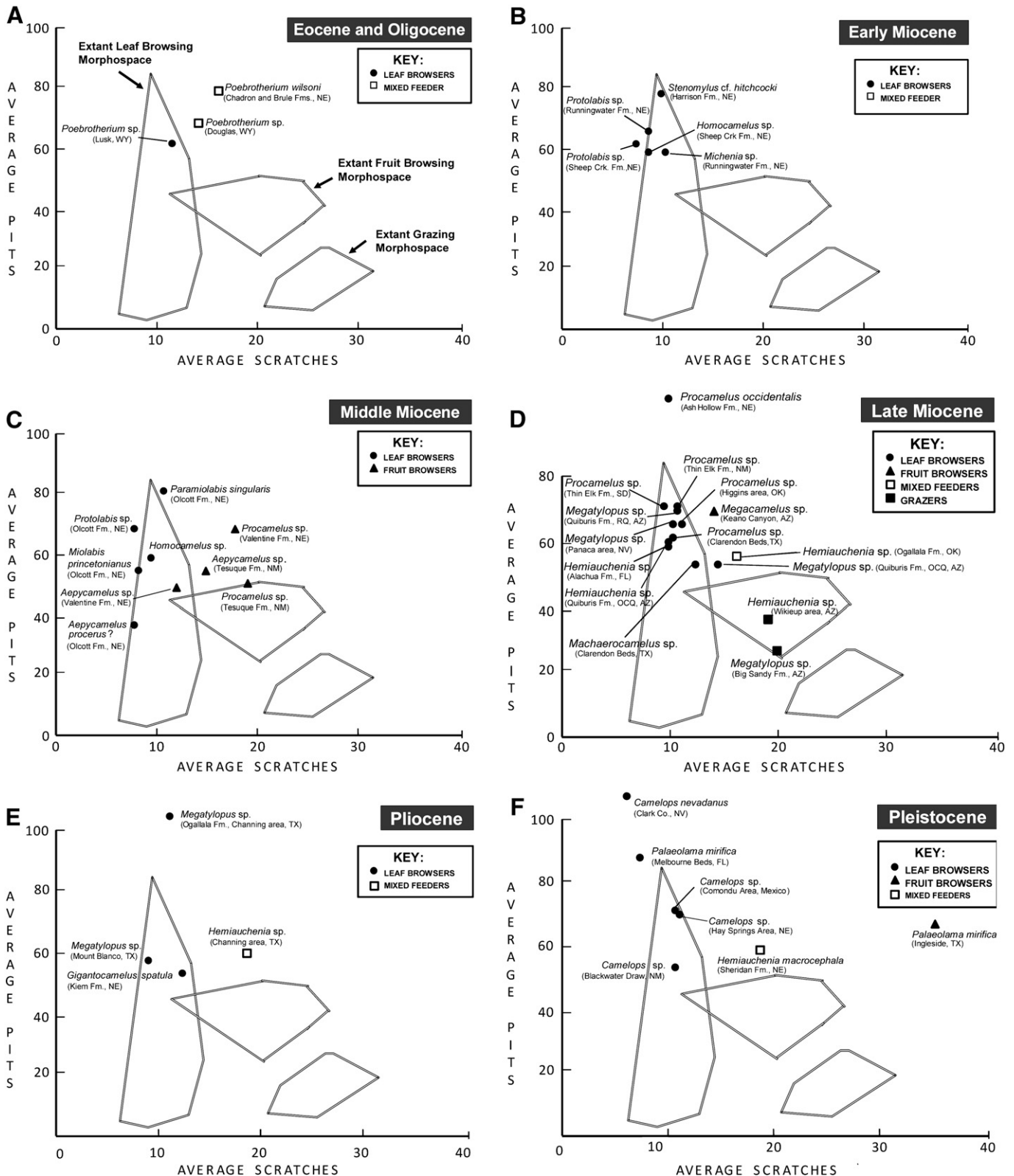
Fig. 6. Bivariate plot of the average number of pits versus average number of scratches in fossil camelids organized temporally. Microwear obtained at 35× magnification with a stereomicroscope (extant data from Solounias and Semprebon, 2002). Convex hulls are drawn around extant leaf browsing taxa and extant grazing taxa for ease of comparison. A. Plot of Eocene and Oligocene camelids. B. Plot of early Miocene camelids. C. Plot of middle Miocene camelids. D. Plot of late Miocene camelids. E. Plot of Pliocene camelids. F. Plot of Pleistocene camelids.

most likely from the beginning lived in areas where grit encroached on their food items (i.e., mostly open habitats). Camelids appear in the late Eocene to Early Oligocene which was about the time of the first

patches of true savanna in North America and coincident with a trend toward aridity on the continent (Retallack, 1992, 2004). In light of this, it is not surprising that the limb morphology of archaic camelids
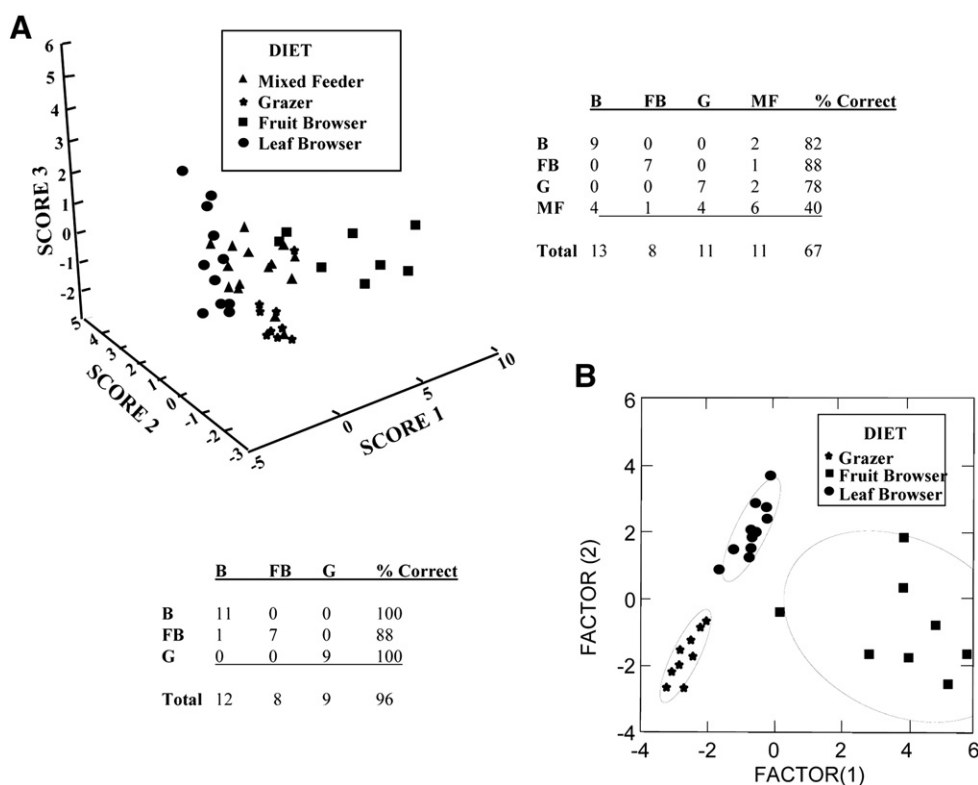
Fig. 7. Canonical score plots and jackknifed classification matrices for the variables that captured most of the differences between extant dietary groups in the discriminant model (average number of pits, average number of scratches, average number of small, medium, and large puncture pits, and percentage of large pits). A. Canonical score plot and classification matrix of the discriminant space of extant leaf browsers, fruit browsers, grazers, and mixed feeders. B. Canonical score plot and classification matrix of the discriminant space of extant leaf browsers, fruit browsers, and grazers, with mixed feeders eliminated.

such as *Poebrotherium* (about the size and build of a goat) reveals that camelids were already adapted to a cursorial, open-habitat existence by the early Oligocene possessing elongated metapodials (and reduced lateral metapodials) and unguligrade posture.

4.2. More advanced camelids

4.2.1. Stenomylinae

More derived camelids evolved some very interesting adaptations. Within the subfamily Stenomylinae are found some of the most hypsodont of the camelids. The early genus *Stenomylus* (late Oligocene–early Miocene) was very widespread (with the exception of Florida) with gazelle like proportions and postcranial adaptations suggesting the occupation of open habitats. Later stenomylines were more restricted in their distribution to more arid habitats (Webb, 1977; Munthe, 1979). *Stenomylus hitchcocki* is the most hypsodont of the early Miocene camelids we studied (Fig. 4) so it is not surprising that the mesowear score for *S. hitchcocki* is quite high relative to the other camelids studied with the exception of the Pleistocene *Camelops* sp. (from the Hay Springs Area in Nebraska) indicating an abrasive element in its diet. Interestingly, *S. hitchcocki* has microwear that indicates a browsing diet. Thus, it is reconstructed here as most likely a "dirty browser" encountering a fair amount of exogenous grit in its diet and most likely occupying an open environment. The sample size for this taxon was large enough to pick up seasonal dietary changes in this locality if they existed. Others (Stirton, 1947; Janis, 1988) have noted that herbivores living in open habitats have a tendency to be more hypsodont, regardless of their preferences for food than those living in closed habitats presumably due to more sand and dust adhering to plant materials consumed. The heavy degree of gouging and high level of pitting found in *S. hitchcocki* provides more evidence of dirty browsing.

4.2.2. Miolabinae and Protolabinae

Miolabines and the more derived protolabines exhibit a shortening of the legs, particularly the metapodials, over time. Consequently, it has been suggested that the protolabines were ground-level feeders (Janis, 1982). Also, *Protolabis* possesses an extremely constricted rostrum and may have possessed highly developed labial and buccal musculature (Honey and Taylor, 1978). These two features have been suggested to indicate a selectivity of low-level feeding perhaps ecologically similar to certain African antelopes which specialize in feeding on certain low-level bushes and grasses (Prothero and Schoch, 2002). It is possible and even probable that the Miolabines and Protolabines were ground-level feeders based on their postcranial morphology. The high pit counts found in these taxa here indicate that they most likely encountered some degree of grit on their food items which might be expected in taxa that fed in open habitats and/or close to the ground. Interestingly however, miolabines and protolabines studied here (Table 3) all display attritive mesowear patterns (i.e., relatively low mesowear scores (Fig. 4B)). It is generally assumed that more rounding of the cusps (i.e., a more abrasive mesowear pattern) would be seen in forms exposed to grit in their food items. However, in reality, it is not at all clear how grit affects mesowear (i.e., how much grit exposure is needed to round cusps) or if it is possible to distinguish abrasion due to grit versus abrasion due to food items. This is why microwear becomes very important in dietary reconstructions. The relatively attritive mesowear patterns seen here may indicate that these forms selectively browsed on very soft food items which did not contribute to dietary abrasion in any appreciable way. Microwear reveals that some grit was most likely consumed with food (i.e., excessive pitting) but presumably not enough to wear the molars appreciably as is seen in *Stenomylus hitchcocki*. Carbon isotopes in dental enamel show *Protolabis* from a variety of Nebraska sites (Clarendonian) to have consumed C3 plants (Christianson, 2007),
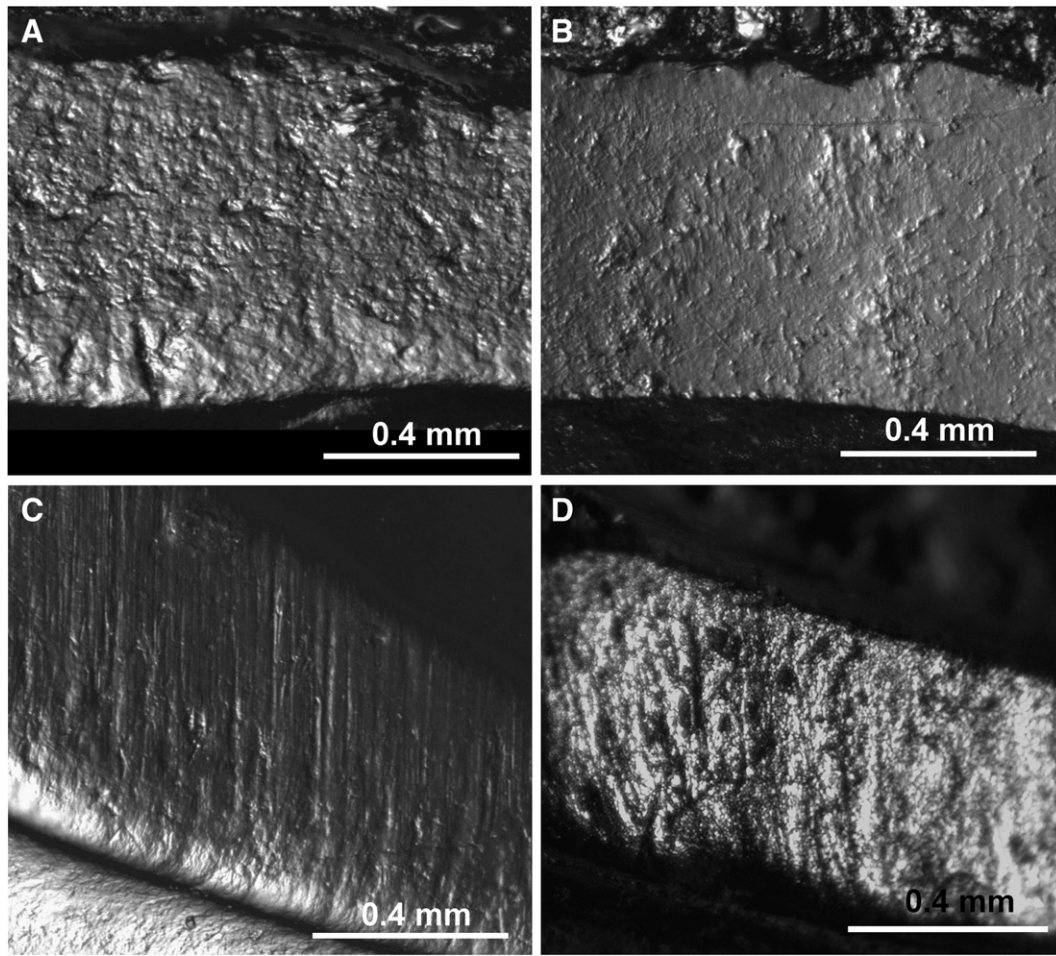
Fig. 8. Photomicrographs of selected fossil camelid tooth enamel at 35× magnification. A = *Machaerocamelus* sp. from the Clarendon Beds of Texas — AMNH 40120; B = *Megatylopus* sp. from the Quiburis FM, Old Cabin Quarry, Arizona — AMNH 47610; C = *Poebrotherium wilsoni* from the Chadron and Brule Formations of Nebraska — AMNH 103244, D = *Aepyceros* sp. from the Valentine FM, Burge Member, Cherry Co. Nebraska AMNH 40427. Scale bar = 0.4 mm.

thus our reconstruction of browsing in miolabines and protolabines is likely.

4.2.3. Camelinae

The Camelinae evolve and begin to radiate in the late early to early middle Miocene (late Hemingfordian and early Barstovian). With their radiation, the more archaic protolabines and miolabines began to decline until they went extinct in the late Miocene (late Hemphillian). It is among the camelines that some truly interesting specializations of the limbs and neck appear that allow some camelids to engage in high-level browsing (e.g., *Aepycamelus*). Therefore, the beginnings of highly elongated limbs and cervical vertebrae in camelids are seen here such as in *Oxydactylus*, the first of the so-called "giraffe-camels". Janis (1982) proposed that this form used its elongated hind limbs in a manner similar to modern gerenuks (*Litocranius walleri*) that stand on their hind legs to reach high levels of browse.

These postcranial features were even more dramatic in *Aepycamelus* which has been suggested to occupy a niche similar to modern giraffes, that is, high-level savanna browsing. Our results support a high-level browsing dietary niche for *Aepycamelus*. *Aepycamelus* sp. from the boundary between the middle and late Miocene (i.e., Barstovian/Clarendonian boundary, Valentine Formation of Nebraska and Tesuque Formation of New Mexico) shows microwear evidence of some fruit and/or seed browsing (very large and deep puncture-like pitting of enamel). A similar microwear pattern was found in the high-level browsing *Okapia johnstoni* by Solounias and Semprebon (2002). Carbon

isotope data from dental enamel corroborates this conclusion and shows a C3 diet in *Aepycamelus* from Nebraska (Christianson, 2007). Consequently, *Aepycamelus* is reconstructed here as most likely occupying a more closed habitat than most of the other fossil camelids studied.

Procamelus is an interesting genus. *Procamelus* sp. from the boundary between the middle and late Miocene (i.e., Valentine Formation of Nebraska and from the Tesuque Formation of New Mexico) both apparently incorporated some fruit and/or seeds into their browse as evidence by some very large puncture-like seed pits etched into their dental enamel (Tables 2 and 3). Interestingly, as mentioned above, *Aepycamelus* sp. from the same localities and same time are doing the same thing (i.e., consuming some fruit and/or seeds). However, the other *Procamelus* taxa analyzed here from the late Miocene apparently browsed mainly on leaves, a pattern consistent with premaxillary shape and enamel isotopes (Dompierre and Churcher, 1996; Feranec and MacFadden, 2006; Christianson, 2007).

Results here show a variety of dietary strategies were employed by *Hemiauchenia*. Microwear reveals that in the early Hemphillian, *Hemiauchenia* sp. apparently relied on browse, a dietary strategy continued into the late Hemphillian but then modified to include grass consumption *Hemiauchenia* is mesodont (Fig. 2) and displays mesowear that is attritive. It falls in a zone occupied by extant attritive mixed feeders. Premaxillary shape analysis of *H. macrocephala* indicates the possibility of a browsing dietary habit (Dompierre and Churcher, 1996) but also would allow it to be a specialized mixed feeder in open habitats (Janis, 1988). The latter conclusion is more

Table 3

Taxon	Locality	Microwear dietary assignment	Mesowear score (= abrasion index)	*Other dietary analyses
Primitive camelids				
Poebrotherium sp.	Lusk, Wyoming	Leaf browser	Low	
Poebrotherium sp.	Douglas, Wyoming	Mixed feeder	Low	
Poebrotherium wilsoni	Chadron/Brule FMs Neb	Mixed feeder	Low	
More advanced camelids				
Stenomylinae				
Stenomylus hitchcocki	Harrison FM Neb	Leaf browser	High	
Protolabinae				
Protolabis sp.	Sheep Creek FM Neb	Leaf browser	Low	[1]Isotopes = C$_3$ feeder
Protolabis sp.	Runningwater FM Neb	Leaf browser	Low	[2]Selective feeding browser
Michenia sp.	Runningwater FM Neb	Leaf browser	Low	
Miolabinae				
Miolabis princetonianus	Olcott FM Neb	Leaf browser	Low	
Aepycamelus sp.	Olcott FM Neb	Leaf browser	Low	
Aepycamelus sp.	Sheep Creek FM Neb	Leaf browser	Low	
Camelinae				
Aepycamelus sp.	Valentine FM Neb	Fruit browser	Low	[1]Isotopes = C$_3$ feeder
Aepycamelus sp.	Tesuque FM NM	Fruit browser	Low	
Procamelus sp.	Valentine FM Neb	Fruit browser	Low	
Procamelus sp.	Tesuque FM NM	Fruit browser	Low	[3]Browsing premaxilla
Procamelus sp.	Thin Elk FM NM/SD	Leaf browser	Low	[1]Isotopes = C$_3$ feeder
Procamelus sp.	Clarendon Beds, TX	Leaf browser	Low	[4]Isotopes = C$_3$ feeder
Procamelus sp.	Higgins Area, OK	Leaf browser	Low	
Hemiauchenia sp.	Alachua FM, Florida	Leaf browser	Low	
Hemiauchenia sp.	Quiburis FM AZ	Leaf browser	Low	
Hemiauchenia sp.	Ogallala FM OK	Mixed feeder	Low	
Hemiauchenia sp.	Wikieup Area AZ	Grazer	Low	
Hemiauchenia sp.	Channing Area, TX	Mixed feeder	Low	
Hemiauchenia macrocephala	Sheridan Area of Neb	Mixed feeder	Low	[5]Microwear = mixed feeder [6,7]Isotopes = mixed feeder
Megacamelus sp.	Keano Canyon AZ	Fruit browser	Low	[1]Isotopes = C$_3$ feeders mostly but occasional C$_4$ grass consumption
Megatylopus sp.	Mount Blanco TX	Leaf browser	Low	
Megatylopus sp.	Big Sandy FM, AZ	Grazer	High	
Megatylopus sp.	Quiburis FM, OC Q., AZ	Leaf browser	Low	
Megatylopus sp.	Quiburis FM, R Q., AZ	Leaf browser	Low	
Megatylopus sp.	Panaca Area, NV	Leaf browser	Low	
Megatylopus sp.	Ogallala FM, TX	Leaf browser	Low	
Camelops sp.	Hay Springs Ar. NB	Leaf browser	High	[5]Microwear = mostly browsing; some mixed feeding
Camelops sp.	Baja CA, MX	Leaf browser	High	[3]Mixed feeding premaxilla
Camelops sp.	Blackwater Draw NM	Leaf browser	Low	
Camelops nevadanus	Locality 100, NV	Leaf browser	Low	
Palaeolama mirifica	Southwestern FL	Fruit browser	Low	[6,7]Isotopes = browser feeder
Palaeolama mirifica	Ingleside, TX	Leaf browser	Low	[6]Mesowear = browser [5]Microwear = browser/mixed feeder
Gigantocamelus spatula	Kem FM, Neb	Leaf browser	Low	
Machaerocamelus sp.	Clarendon Beds, TX	Leaf browser	Low	

[1]Christianson, 2007.
[2]Honey and Taylor, 1978.
[3]Dompierre and Churcher, 1996.
[4] Feranec and MacFadden, 2006.
[5] Dompierre, 1995.
[6,7] Meachen, 2003, Kohn et al., 2005.
*Other authors' studies are occasionally only specific to the genus level or general locality of taxa studied here.

consistent with results determined here (bimodal scratch distribution) and with SEM microwear results (Dompierre, 1995) and carbon isotopic data from dental enamel (Meachen, 2003; Kohn et al., 2005).

Results on the late Hemphillian *Megacamelus* sp. indicate a browsing adaptation with some fruit and/or seed consumption based on microwear results. However, the high pit counts and mesodont cheek teeth of this taxon implies the possibility of open-habitat dirty browsing and/or the inclusion of more abrasive dietary items in its trophic repertoire than browse as *Megacamelus* sp. from the Devil's Airstrip Quarry in Nebraska (late Hemphillian) has carbon isotope values in its dental enamel that are less negative than typical browsers, hinting that some grass may have been consumed at times by *Megacamelus* (Christianson, 2007).

A diversity in diet is apparent in *Megatylopus*. Results on late Miocene (late Hemphillian) and Pliocene (Blancan) *Megatylopus* indicate the majority of forms were "dirty browsers" although *Megatylopus* sp. from the Big Sandy Formation of Arizona apparently grazed. The relatively high abrasion mesowear results for this taxon (Table 3) is consistent with grass consumption. Results reported here are concordant with enamel isotope results which reveal mostly C$_3$ feeding but that some C$_4$ food items were consumed (Christianson, 2007).

Camelops is also an interesting genus in terms of the variety of dietary strategies apparently employed. *Camelops* sp. from the Hay Springs area of Nebraska has results consistent with high abrasion (i.e., "dirty") browsing, whereas other *Camelops* sp. (Comondu Area
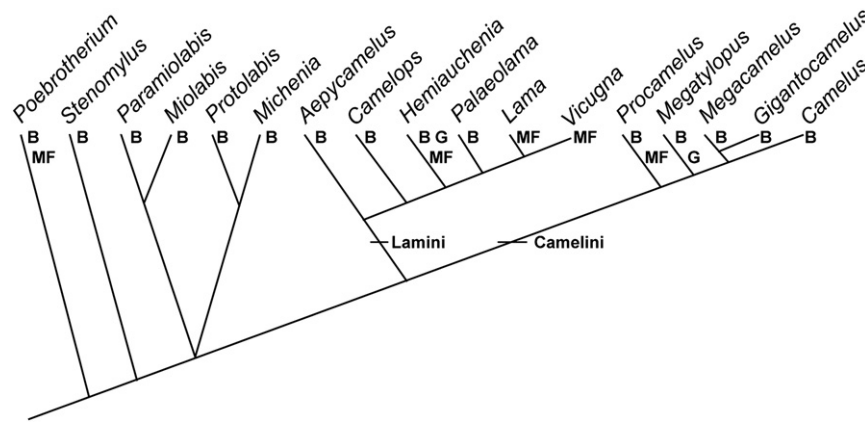
Fig. 9. Phylogeny of the Camelidae and dietary assignation resulting from dental microwear analysis. Abbreviations: B = browser; G = grazer; MF = mixed feeder.

Baja California, Mexico, Blackwater Draw New Mexico, and Locality 100, Nevada) have results typical of low abrasion (i.e., "clean") browsers. Dompierre (1995) also reconstructs *C. nevadanus* as a browser based on SEM microwear.

However, results on other species of *Camelops* not analyzed here, indicate that some grass may have been consumed by some forms (Table 3). Also, the degree of hypsodonty found in some *Camelops* taxa has led to an assumption of grazing in this taxon. However, Akersten et al. (1988) found that the hypsodont Pleistocene *Camelops* from Rancho La Brea had preserved food materials from its teeth that were nonmonocotyledon (i.e., not grass). Thus, tall crowned teeth may allow an animal to eat abrasive foods such as grass but do not limit them to such a diet and allow for an increased dietary breadth (Feranec, 2003).

Very intriguing results were obtained by Vetter et al. (2007) on *Camelops* sp. from Southern Nevada. The ^{13}C values from late Pleistocene *Camelops* indicates the highest proportion of C_4 plants consumed by the megafauna studied including *Mammuthus*, *Equus* and *Bison*. However, the authors do not reconstruct *Camelops* as a grazer. This is because independent vegetation records and paleoclimatological reconstructions from this area and time indicate that there was a low abundance of C_4 grasses but rather the halophytic C_4 shrub *Atriplex* was a substantial component of the Mojave Desert vegetation. These results are concordant with those of Coltrain et al. (2004) that found no evidence for reliance on C_4 grasses at Rancho La Brea. It is well known that modern camelids prefer halophytic plants (including *Atriplex*). This study is very important as results dictate that caution should be employed when concluding that grass is the only explanation for C_4 isotope values in fossil enamel. It appears that *Camelops* may have had a preference for salty plants in Nevada and consumed browse material with a high proportion of C_4 halophytic shrubs.

Paleolama mirifica has been reconstructed as a browser most likely occupying closed canopy deep forest (Meachen, 2003; Kohn et al., 2005). SEM microwear (Dompierre, 1995) however reconstructs *P. mirifica* (California, Rancholabrean) as an intermediate feeder. However, in this study, only two teeth were analyzed and one specimen showed low numbers of scratches typical of browsers, while the other showed higher scratch counts. Solounias and Semprebon (2002) have shown that fruit browsers often have microwear that resembles mixed feeders in terms of bimodal scratch distributions. Low magnification stereomicrowear analysis has revealed that fruit and seed coats apparently can scratch dental enamel much like grasses (Solounias and Semprebon, 2002; Semprebon et al., 2004a). What separates mixed feeders from fruit browsers is the presence of seed pits in the latter which *P. mirifica* possesses. *P. mirifica* from

Florida and Texas are therefore reconstructed here as browsers. *P. mirifica* from the Melbourne Beds of Florida has wear consistent with leaf browsing while *P. mirifica* from Ingleside Texas apparently incorporated some fruit and/or seeds into its browse. These results are concordant with the fact that *Palaeolama* possesses cheek teeth that are the lowest crowned of the Lamini (Honey et al., 1998).

Results for *Gigantocamelus spatula* (Pliocene–late Blancan) from the Kem Formation of Nebraska are quite preliminary due to our small sample size ($N = 3$). However, microwear results indicated a probable dirty browsing strategy.

Unlike the sample for *Gigantocamelus* sp., our sample for the late Miocene *Machaerocamelus* sp. from the Clarendon Beds of Texas is quite large. Once again, a relatively dirty browsing pattern is most likely.

5. Conclusions

5.1. Camels exploited open habitats early on in their evolution and preferred such habitats throughout most of their evolutionary history

Camels apparently both browsed and grazed in the late Eocene/early Oligocene (e.g., *Poebrotherium wilsoni*) thus most likely occupying relatively open habitats. Wooded grasslands were most likely available in North America by about 32 million years ago (late Eocene/early Oligocene) and open grasslands by the early Oligocene (Retallack, 1992, 2004) based on paleosol data. Paleosol data from the Great Plains indicate that scattered bunch grasses and shrubs were present in the Oligocene as well as short grass prairie (Retallack, 1997) although phytolith data suggests that modern open-habitat grasslands did not occur until the early Miocene (Strömberg, 2004a,b). The camels studied here consistently display low-scratch results typical of browsing forms yet they also display heavy pitting and often gouging of their enamel surfaces, as well as relatively coarse scratch textures and moderate crown height augmentation throughout their evolutionary progression indicating the occupation of more open habitats than closed-habitat browsing forms.

5.2. Crown height in camels is not correlated with an increase in grass consumption

Average scratch counts are very consistent through time in these fossil camelids and are characteristically low. Also, mesowear scores are consistently low regardless of crown height and are atypical for grazing forms. These results are indicative of an overall dietary strategy in camels through most of their evolutionary progression that lacks significant grass consumption. Thus the highest crowned taxa

studied (*Stenomylus* and *Camelops*) have browsing type microwear and mesowear and forms with toothwear suggestive of some grass consumption (*Poebrotherium* and *Megatylopus*) are no more hypsodont than the others (Fig. 3). Browsing apparently was the mainstay of most ancient camels.

5.3. Dietary abrasion is concordant with established trends in aridity and temperature in the North American Tertiary and Quaternary

Camel hypsodonty and mesowear decreases in the middle Miocene, a time when fruit and/or seeds apparently were added to browse for both *Aepycamelus* sp. and *Procamelus* sp. from the Tesuque Formation (New Mexico) and Valentine Formation (Nebraska) based on microwear results and a time when closed habitats were more pervasive in the Great Plains (Janis, 1993). This trend toward frugivory decreases in the late Miocene but *Megacamelus* sp. from Keano Canyon (Arizona) apparently incorporated fruit into its diet as did *Palaeolama mirifica* from the Melbourne Beds (Florida).

In the late Miocene, the most obvious shift in camelid results are seen (Fig. 4). A distinctive shift is apparent in the abrasiveness of browse, in augmentation of crown height, and in the appearance of the first grazing forms. Miocene mammalian dental enamel isotopes help to elucidate the type of vegetative biomass available to camels and can serve as a proxy for diet to interpret the abundance of C_3 and C_4 biomass in the Great Plains at this time. Carbon analysis of $\delta^{13}C$ isotopes in tooth enamel of seven different Camelidae genera from the Barstovian, Clarendonian and Hemphillian of Nebraska were analyzed by Christianson (2007). Results showed a shift from the consumption of mainly C_3 plants to the consumption of both C_3 and C_4 plants in the late Miocene in both the Camelidae and the Equidae studied. Both the horses and camels studied consumed predominantly C_3 vegetation until about 6.6 million years ago, when some began to consume C_4 as well as C_3 vegetation. These values are consistent with the paleosol isotope record for the Great Plains which indicates an increasing proportion of C_4 biomass beginning between 6.4 and 4.0 million years ago (Tieszen et al., 1997; Fox and Koch, 2003) and with the results of this study.

The end of the Miocene signaled the end of the great camel radiation and also a worldwide climate event called the Messinian crisis which entailed oceanic changes, Antarctic glaciations, and rather dramatic changes in worldwide climate (i.e., a global cooling event) (Prothero and Schoch, 2002) with concomitant vegetational changes. Consequently, the remaining forests and leafy-type vegetation were replaced by dry grasslands and steppe vegetation (Wing, 1998; Graham, 1999), leading to extinction of species and genera within the Camelidae as well as many of the other animals which were adapted to the mixed grasslands and woodlands of the Hemphillian. Microwear also records a definitive shift toward coarser browse and/or more grit encroachment on food items as well as the appearance of true grazing (e.g., *Hemiauchenia* sp. from the Wikieup Area of Arizona and *Megatylopus* sp. from the Big Sandy Formation of Arizona) for the first time.

Hemiauchenia continued its trend toward grass consumption into the Pliocene (*Hemiauchenia* sp. from the Channing Area of Texas) and Pleistocene (*H. macrocephala* − Sheridan Formation in Nebraska). Hypsodonty and mesowear also decreased in camelids in the Pleistocene to the Recent, a trend also noted by Semprebon and Rivals (2007a) for fossil antilocaprids. Paleobotanical evidence shows that the early Pliocene of North America was slightly warmer than the late Miocene (Axelrod, 1985, 1992; Wolfe, 1985; Webb and Opdyke, 1995; Wing, 1998; Graham, 1999) but much drier which led to treeless grasslands or steppe habitats (Prothero, 2006). Gouging of enamel is reduced in particular in the Pliocene and moderately so in the Pleistocene − the same pattern observed in terms of large pitting. Gouging (large irregular chunks chipped off of enamel) has been interpreted as most likely due to grit exposure on food items

(Solounias and Semprebon, 2002; Semprebon et al., 2004b) and a reduction in gouging may indicate a shift toward cleaner browse after the late Miocene.

By the beginning of the late Pliocene, the earth quickly cooled and by the end of the Pleistocene, the last remaining forms (e.g., *Palaeolama mirifica*, *Hemiauchenia macrocephala*, and *Camelops hesternus*) went extinct in North America (Kurten and Anderson, 1980) leaving only the Old World camelines (i.e., *Camelus*) and South American llamines (*Lama* and *Vicugna*).

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