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Advances in the Reconstruction of Ungulate Ecomorphology with Application to Early Fossil Equids

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ABSTRACT

A new and greatly simplified methodology for the assessment of the dietary adaptations of living and fossil taxa has been developed which allows for microwear scar topography to be accurately analyzed at low magnification (35×) using a standard stereomicroscope. In addition to the traditional scratch and pit numbers, we introduce four qualitative variables: scratch texture, cross scratches, large pits, and gouges, which provide finer subdivisions within the basic dietary categories. A large extant comparative ungulate microwear database (809 individuals; 50 species) is presented and interpreted to elucidate the diets of extant ungulates. We distinguish three major trophic phases in extant ungulates: traditional browsers and grazers, two phases represented by only a few species, and a browsing-grazing transitional phase where most species fall, including all mixed feeders. There are two types of mixed feeders: seasonal or regional mixed feeders and meal-by-meal mixed feeders. Some species have results that separate them from traditional members of their trophic group; i.e., browsers, grazers, and mixed feeders. Duikers are unique in spanning almost the entire dietary spectrum. *Okapia*, *Tapirus*, *Tragulus*, and *Moschus* species have wear similar to duikers. Proboscideans fall in the browsing-grazing transitional phase, as do the two suids studied. The latter differ from each other by their degree of rooting.

Archaic fossil equids spanning the supposed browsing-grazing transition were compared to extant ungulates. Two major clusters are discerned: (1) *Hyracotherium* has microwear most similar to that of the duiker *Cephalopus silvicultor* and was a fruit/seed eating browser. (2)

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Mesohippus spp., *M. bairdii*, *Mesohippus hypostylus*, *Meso-Miohippus* (a transitional form larger than *M. bairdii*), *Parahippus* spp., and *Merychippus insignis* differ from *Hyracotherium* and are most similar to the extant *Cervus canadensis*. Group (2) is characterized by fine scratches which are the result of C3 grazing, an initial phase of grazing in equids which most likely did not occur in open habitats. Finer differentiation of group (2) diets shows a dietary change in the expected direction (toward the incorporation of more grass in the diet) and follows the expected evolutionary transition from the Eocene to the Oligocene and early Miocene. Consequently, these equid taxa are reconstructed here as mixed feeders grazing on forest C3 grasses. The finer dietary differentiation shows a progressive decrease in the number of scratches and pits. *Mesohippus* has the most pits and scratches, followed by *Parahippus*, and then *Merychippus* (which has the least). The taxon incorporating the most grass into its dietary regime in this array is *Merychippus*. In *Mesohippus-Parahippus* versus *Merychippus*, differences in tooth morphology are major but microwear differences are slight.

INTRODUCTION

Ungulates have diversified in the past and present into numerous niches. Being herbivorous, their dietary adaptations are closely linked to vegetation realms. Similarly, various locomotor adaptations have paralleled changes in ecology. The present study has two major objectives: (1) to develop a better understanding of living ungulate dietary adaptations through tooth microwear analysis using a new methodology (light microscope and low magnification); (2) to apply the new microwear technique to archaic fossil equids from North America in order to discern their most probable dietary adaptations. We investigate *Hyracotherium*, *Mesohippus*, *Parahippus*, and *Merychippus*–the genera expected to span the browsing-to-grazing evolutionary transition.

The adaptations and evolution of ungulates are fascinating (Janis, 1982; Grasse, 1955; Prothero and Schoch, 1989; Vrba and Schaller, 2000). Pivotal works by Janis (1982; 1988), Webb (1977, 1983), and Span et al. (1994) have brought into focus some of the general ideas proposed by Simpson (1951), Osborn (1910), Stirton (1947), and others. In summary, primitive low-crowned ungulate species are thought to have evolved into higher crowned ones as their diets changed from browsing to grazing. This change has been thought to parallel the replacement of rainforests and subtropical forests by habitats with drier ecologies, such as temperate woodlands, savannas, and grasslands. Most ungulate species (especially equids) supposedly responded to such climatic and vegetation changes by changing their dietary and locomotor adaptations accordingly (Rensberger et al., 1984; MacFadden, 1992).

Ungulate dietary research has recently progressed further with microwear studies (Caprini, 1998; Janis, 1990; Solounias and Moelleken, 1992a, 1992b, 1993a, 1993b, 1994; Hunter and Fortelius, 1994; Solounias et al., 2000a;), hypsodonty studies (Fortelius, 1985; Janis, 1988; Janis and Fortelius, 1988; Solounias et al., 1994), masseter studies (Solounias et al., 1995), foraminal studies that relate size of cranial nerves five and seven to diet (Solounias and Moelleken, 1999), and the novel mesowear method that relates relative sharpness of tooth cusps to diet (Fortelius and Solounias, 2000).

Past tooth microwear analyses have examined enamel surfaces at high magnification. The pioneering electron microscope studies by Walker et al. (1978) and Rensberger (1973, 1978) demonstrated the usefulness of this method. Since then, others have studied tooth microwear using the scanning electron microscope (SEM) to understand various aspects of primate, rodent, and ungulate dietary adaptations (see Teaford, 1988 and Janis, 1995 for reviews). Microwear (scratches and pits) has been used to differentiate browsers, grazers, and mixed feeders in extant ungulates and in the ruminant fossil record (Solounias and Moelleken, 1992a, 1992b, 1993a, 1993b, 1994), sometimes with surprising results. For example, Solounias et al. (1988) showed that *Samotherium* was a mixed feeding or possibly a grazing giraffid. More recently, isotopes and microwear have been used to show dietary differentiation and niche partitioning in a group of presumably coexisting fossil equids from the Bone Valley locality of Florida. Among these species, *Dinohippus mexicanus*, although hypsodont and close to modern *Equus*, turned out to be a browser (MacFadden et al., 1999). Microwear proved useful because it showed that *Samotherium*, a brachydont species, was a mixed feeder-grazer, whereas *Dinohippus*, a hypsodont species, browsed. These findings are contrary to expectations based on crown height alone. Microwear research, although already demonstrated to be very useful, has been constrained and underutilized primarily because of logistical problems involving the time and expense required to obtain and evaluate data with a scanning electron microscope.

In the present study, we have developed and utilized a new low-magnification method for microwear. It is possible to completely study a large sampling of tooth specimens from a species with this technique in a few hours. With conventional scanning electron microscopy methods, such an analysis would most likely require close to a month of analytical time. Given the advantage of the new method, we have examined the teeth of numerous extant ungulates to better understand their actual dietary habits. Throughout this work, it has become clear that the ecomorphology of modern ungulates needs to be better understood. Our study offers a clear step toward such an improved understanding. In addition, this methodology has clearly differentiated interesting new dietary patterns and has provided evidence that the trophic scenario is more complex than was previously supposed.

The new microwear methodology greatly simplifies the laboratory work, as it requires only a standard light stereomicroscope. Also, it circumvents previous technical problems inherent in the microwear process such as time-investment problems and expense concerns. The new method makes it possible to assay a greater number of specimens within a species, as well as to increase the number of taxa which can be assessed, thereby allowing for a larger and broader representation of animals from different continents. The larger sample sizes allow for a more critical and statistically significant examination. These improvements should encourage other researchers to apply the microwear technique in a much broader manner than it has been utilized thus far.

Because of these advancements, a new and greatly expanded comparative microwear database for extant ungulates was a byproduct of this study. This provided a mechanism for the examination of the most probable dietary adaptations of five critical fossil equids which temporally span the transition from brachydont (low tooth-crowned), and presumably browsing forest taxa, to those which possessed a more modern type of equid tooth (hypsodont or high-crowned with cementum), ostensibly used for grazing and the invasion of more open grassland habitats. In this way, it was envisioned that the browsing-to-grazing transition in the evolutionary scenario of horses (equids), so often discussed in the literature, would be elucidated.

Before we expand into the equid issues, we point out that the new microwear method has been preliminarily related to mesowear. The mesowear method is fast and simple and is based on relative tooth facet development. This method is based on the physical properties of ungulate food items as reflected in the relative amounts of attritive and abrasive wear that they cause on the dental enamel of occlusal surfaces. Mesowear analysis involves scoring the buccal apices of molar tooth cusps (in lateral view). Tooth apices are characterized as sharp, rounded, or blunt, and the valleys between them are noted as either high or low. Mesowear is a signature of long periods (prolonged wear) during the lifespan of an individual (Fortelius and Solounias, 2000). Microwear, on the other hand, changes quite rapidly, and most likely reflects the last meal consumed by a species. Future research will more fully integrate these two methods. At present, we favor both methods for understanding the dietary habits of ungulates. Both are simple and rapid, and very large sample sizes can be easily attained. However, additional work needs to be done to understand how to fully integrate the dietary information retrievable from microwear and mesowear.

Crown height has also often been related to diet. Janis and Webb's original studies have focused on the obvious differences in tooth crown height between ungulates in various dietary categories. It is true that certain generalities exist regarding crown height; that is, primitive species are often low-crowned (brachydont) and advanced grazing species are generally high-crowned (hypsodont). Thus, in general, brachydont species browse and hypsodont species graze (Janis et al., 2000). However, microwear and mesowear studies have shown that hypsodonty does not correlate precisely with observed diets in ungulates (Solounias et al., 1988; MacFadden et al., 1999; Fortelius and Solounias, 2000). The present study confirms that crown height does not often correlate well with diet. To explain this discrepancy, we think that crown height is a long-term adaptation passing into deep time for a particular species and may be related to both attrition (tooth-on-tooth contact) and abrasion (food-on-tooth contact), or more precisely, it may be related to the interactive result of attrition and abrasion (Fortelius and Solounias, 2000). In addition, the current study suggests that excessive grit encountered in the diet is most likely a major contributing factor in the development of hypsodonty in certain species. This finding substantiates Janis (1988), who proposed that dust and grit accumulation might be factors in the evolution of hypsodont teeth, as is the abrasive silica of grasses. These findings make hypsodonty, a morphological feature relating to deep time adaptation of a particular species, an even more interesting, but also more problematical, factor in dietary interpretations.

The fossil record and the adaptive radiation of equids during the Cenozoic of North America are impressive. There are numerous morphologically different species in many localities throughout the Cenozoic. During the maximal equid diversity in the late Miocene, some fossil localities show as many as 12 sympatric species (MacFadden, 1992). Thus, several species of equids in the past coexisted in a fashion similar to what is seen with bovids and cervids today.

A popular, central theme of equid evolution involves tracking environmental changes from closed to open habitats through equid morphology. As previously stated, these changes have been assumed to be associated with changes in dietary adaptations from browsing to grazing morphologies and/or the invasion of open habitats (MacFadden, 1992: Janis, 1982), as well as locomotor changes toward more cursorially adapted postcrania. Equids supposedly responded to such climatic changes and changed their dietary and locomotor adaptations accordingly (Rensberger et al., 1984; MacFadden, 1992; Spaan et al. 1994). More recent equids are perceived of as open-country grazers, as modern *Equus* does not inhabit forested areas and it subsists on grass (Slade and Godfrey, 1982). Interestingly, although many key equid species have been studied from systematic and stratigraphic perspectives, their detailed paleoecology remains mainly unknown.

Rensberger et al. (1984) have shown differences in the dentition of equids that relate to dietary changes. Bernor et al. (1980) and Woodburne (1982) have also shown the significance of the various ecological aspects of equid evolution. Caprini (1998) examined microwear differences in many fossil equids using the scanning electron microscope; however, this work was limited to one or a few individuals per species. Thus, these differences cannot be evaluated statistically. Previous microwear analysis identified *Merychippus* (previously known as *Cormohipparion*) *goorisi* and *Merychippus insignis* as mostly grazing taxa, while *Cormohipparion quinni* (formerly *C. sphenodus*) and *Cremohipparion proboscideum* were found to be mixed feeders (Hayek et al., 1992: table 4). Fortelius and Solounias (2000) have shown that mesowear analysis roughly agrees, with *Cormohipparion goorisi* being the most grazing species and *C. quinni* being an abrasion-dominated mixed feeder. *Merychippus insignis* was found to have slightly different results by the two methods: abrasion-dominated mixed feeder according to mesowear, and grazer according to microwear. The microwear sample of *Cremohipparion proboscideum*, however, contained only five individuals; consequently, it is possible that it did not show the browsing signal recorded by mesowear analysis.

The radiation of the Equidae can be organized into a series of general trends (Matthew, 1926; Simpson, 1951; MacFadden and Hulbert, 1988). Evolution from *Hyracotherium,* one of the earliest equids, to later forms involved both dietary and locomotor changes. *Hyracotherium* was relatively small (MacFadden, 1986), with a dorsally convex back, a four-digit manus, and a three-digit pes. Also, members of the Hyracotheriinae had relatively primitive skull morphology and brachydont molars with fairly simple triangular premolars (i.e., relatively non-molariform). Later equids, such as *Mesohippus*, were larger sized, with a more horizontal or even dorsally concave back, a three-digit manus and pes (tridactyl condition), more elongated metapodials, and other cursorial adaptations (e.g., tight locking of articular surfaces). Their dentitions were more advanced as well, with transverse wavy lophs, a buccal cutting edge, and complete molarization of the premolars. Later still, in *Merychippus*, an even larger body size was attained (MacFadden, 1986), as well as a slender, more cursorial body form (though still tridactyl). Importantly, in *Merychippus*, molars became more modern in appearance (mesodont with well-developed cementum between lophs), with cusps positioned in the same basic patterns as seen in modern horses (*Equus*) (Stirton, 1947; Simpson, 1951; MacFadden and Hulbert, 1988; MacFadden and Hulbert, 1990; Bernor et al., 1989,1997; Prothero and Schoch, 1989; Hulbert and MacFadden, 1991; MacFadden et al., 1991; Spaan et al., 1994). In the present study, we investigate the dietary changes during the evolutionary transition from *Hyracotherum* to *Mesohippus*, and ultimately to *Parahippus* and *Merychippus*.

MATERIALS AND METHODS

We developed an extensive extant comparative ungulate microwear database (809 individuals; 50 species). Appendix 1 and the Acknowledgments section show the museums and collections utilized for this study. For the genus *Tragulus*, we grouped three species together because of the small number of individuals. Thus, the diet of *Tragulus* is only generally examined. The selection of the fossil species was exploratory, as more detailed research is under way. For example, *Hyracotherium* spp., *Mesohippus* spp., and *Merychippus insignis* are represented by large specimen numbers, whereas *Meso-Miohippus* and *Parahippus* sample sizes are smaller and represent a more preliminary examination of these equids. We used a sample of *Hyracotherium* spp. sensu lato to examine the general diet of this type of small and early bunodont equid. With *Mesohippus*, a taxon that possesses more lophodont teeth than *Hyracotherium*, we have gathered a broader sample to see if different species of *Mesohippus* enjoyed diverse diets. We report on *Mesohippus* spp., *M. bairdii*, *M. hypostylus*, and *M. westoni*.

A larger sized species than *M. bairdii*, labeled as *Meso-Miohippus* in the AMNH collections, was included because the dental morphology was similar to *Mesohippus bairdii*, yet there was a substantial difference in size between the two. Our experience shows that species of differing sizes but similar tooth morphologies generally have some differences in diet. A small sample of what is termed *Parahippus* spp. was included to explore the possibility of dietary differences between a large sized *Mesohippus* and a similar-sized *Parahippus*. There may be more than one species included in *Parahippus* (MacFadden, personal commun.), and our study is not designed to thoroughly address this issue. Finally, *Merychippus insignis* (Olcott Formation) was included as one of the first equids which added cementum to its dentition and which achieved substantial hypsodonty. We expected *Merychippus* to have a different diet from the other species sampled in the study for the above reason. We also include *Merychippus goorisi* microwear data from a previous study (Hayek et al., 1992).

PREPARATION OF DENTITIONS: Examination of microwear was done on the second enamel band of the paracone of upper M2 (fig. 1A). For both extant and extinct specimens, the paracones were covered and soaked with a shellac remover (Zip-Strip) using cotton swabs (Q-tips on wooden stems, hospital nonsterile type). After 30 minutes, the teeth were wiped with 95% alcohol several times using cotton balls and after this with cotton swabs. When completely dry, the surface of the teeth was molded twice using a high-precision polyvinylsiloxane dental impression material. The first mold was applied as a final cleaning step and then discarded, as inevita-

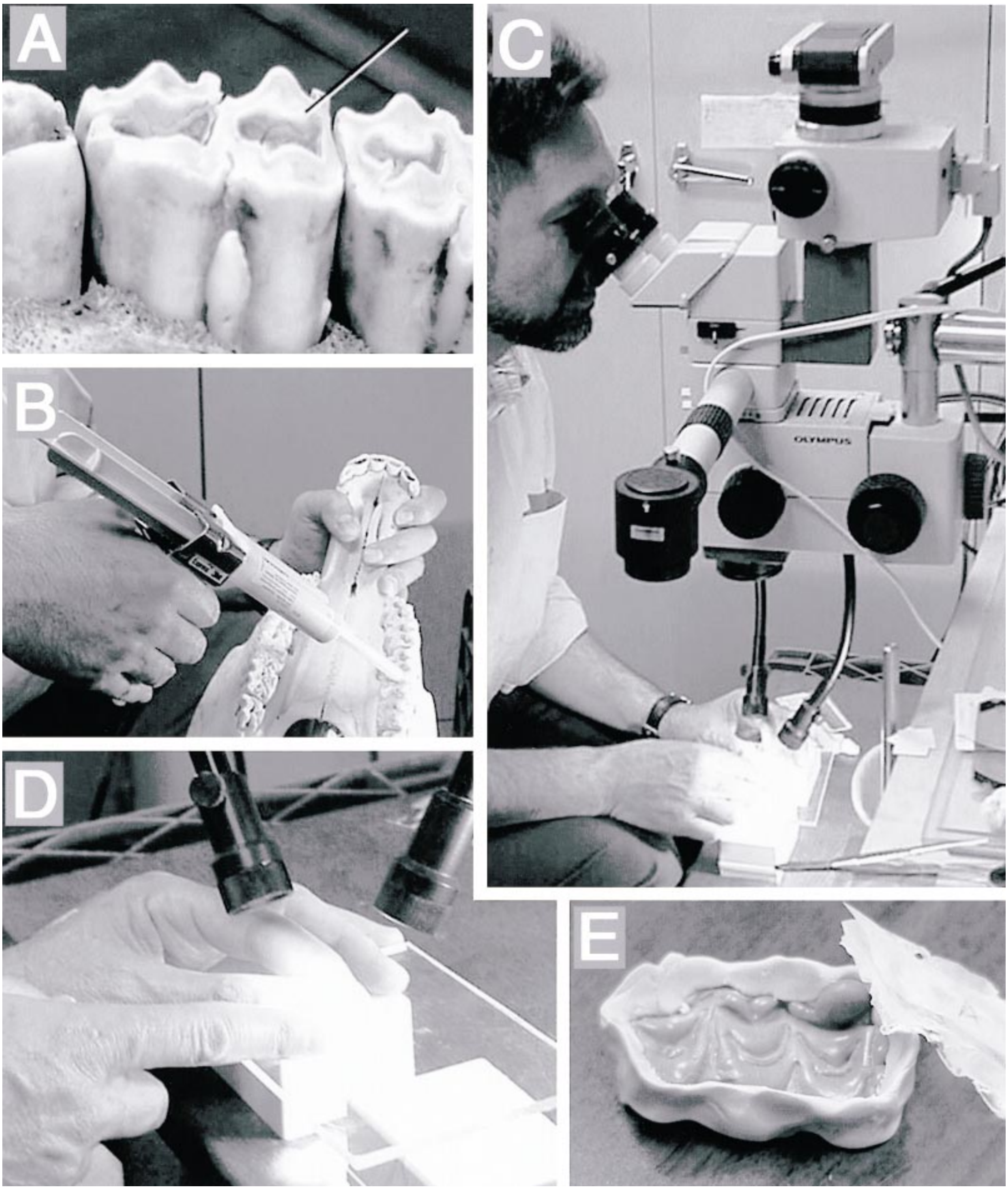

Fig. 1. **A:** Cow molar showing second band of enamel where all microwear samples were taken. **B:** Applicator gun. **C:** Olympus SZH 10 stereomicroscope. **D:** Plexiglas stage used for reflected illumination from table surface. **E:** Typical mold with surrounding wall to hold fluid epoxy and epoxy cast of the tooth surface.

bly some debris adheres to the first mold when it is removed (fig. 1B).

The second mold was larger (covered entire paracone including lingual and buccal sides) and was subsequently surrounded by a thin ribbon of lab putty that was knitted by hand and applied to the edge of the mold (fig. 1E). This ribbon formed a containing wall that prevented liquid epoxy resin from spilling out when it was subsequently applied (fig. 1E). This mold was used for making clear epoxy casts (high- quality epoxy resin and hardener at ratios 5:1. The molds were filled up rather high with epoxy to avoid the bottom surface of the resulting cast from being in close proximity with the examining surface, thus potentially interfering with the visualization of microwear examined on the occlusal surface through a transparent tooth cast. The epoxy was mixed well and then centrifuged for approximately 3–5 minutes before pouring. Centrifuging the mixture eliminates bubbles and also helps the epoxy set better and more quickly. Pouring epoxy resin into the welled molds was done carefully by dribbling the liquid along the margin of the mold and then letting it stream into place. This simple precaution prevents bubbles from forming within crevices of the enamel ridges, which would potentially interfere with the visualization of enamel scar features.

Clear epoxy tooth casts were examined at 35× magnification using an Olympus stereomicroscope (fig. 1C, D). SEM casts from previous studies that had been coated with conductive metals (gold or palladium) were also examined under the light microscope. The SEM tooth casts were examined again and recalibrated at 35× (old counts at 500× were not used). All specimens were from museums and represent wild adults (excessively old or young individuals were not sampled). Upper M2 paracones were analyzed in teeth where M1-M3 were in occlusion. Such animals are more likely to have been eating representative foods before they died than young, old, or zoo animals. The same selection parameters were used when choosing individual fossil specimens. The new clear epoxy casts and recycled SEM casts were combined to assemble an extensive extant ungulate microwear sample.

Microwear analysis was done using a standard light stereomicroscope and oblique lighting on 50 taxa of living ungulates of known diets and on 5 fossil equid taxa. All prior microwear studies have used 500× magnification and a scanning electron microscope.

LIGHTING CONDITIONS AND PHOTOGRAPHY: The light regime employed proved to be of critical importance, and some skill was required for obtaining the best visibility of features. Microwear pits and scratches were visually identified and counted on tooth casts rather than directly on actual teeth. The high reflectivity of enamel surfaces results in excessive glare when light is shined on them, masking many enamel scars. Epoxy casts are less shiny on their surfaces than is dental enamel, and the procedure works much better using such casts than using actual teeth. However, it is highly likely that with the application of special filters, this technique might be amenable to examining microwear directly on actual tooth surfaces, thus eliminating the necessity for making molds or casts, simplifying the procedure even further. This would allow for the examination of the dietary attributes of fossil fauna directly at a dig site.

The best results were obtained when the light source was allowed to shine through the cast at a shallow angle to the occlusal surface. The casts can also be placed on a small transparent stage made of plexiglass and then illuminated from below by reflected light off the table (fig. 1D). Epoxy casts that have already been coated with conductive metals for SEM studies are also suitable, but the intensity of the light source must be reduced and light must strike the cast at a low angle across the metal-coated surface. Nongrease artist clay may be used to anchor tooth casts once the desired lighting conditions have been obtained.

While adjusting the manner in which light strikes the cast (i.e., angle of incident light beam and intensity), the visualization of microwear features can vary from none visible to a few or many, depending on the experience of the researcher. In order to see small features (e.g., small pits), some minor adjustments in lighting position and intensity are often necessary. In addition, the angle of light often needs to be altered slightly to view pits versus scratches. A darkroom also greatly facilitates the process of achieving maximal resolution of microwear features. With the proper adjustment of the lighting parameters, microwear becomes clearly and immediately visible, although microphotography is somewhat challenging due to the

TABLE 1
Microwear Data, Comparative Database

Taxon	Abbrev.	N	Hypso.[a]	Aver. pits	Aver. scratches	% Cross scratches	% Large pits	% Gouges	% Fine scratches	% Coarse scratches	% Mixed scratches
EXTANT SPECIES											
Browsers, Fruit Dominated											
Cephalophus niger	NI	7	Bra	33	9.43	100	71.43	57.14	42.86	0	57.14
Tapirus terrestris	TERR	22	Bra	27.73	17.23	77.27	86.36	4.55	22.73	22.73	54.54
Cephalophus dorsalis	DR	21	Bra	39	19.55	76.19	85.71	80.95	0	61.91	38.1
Cephalophus silvicultor	SL	15	Bra	20	19.83	66.67	73	26.67	33.33	0	66.67
Okapia johnstoni	OJ	25	Bra	34.6	20.68	84	84	56	8	56	36
Tragulus spp.	TRA	11	Bra	30	22.09	54.55	100	0	9.09	63.64	27.27
Moschus moschiferus	MO	3	Bra	37	25	100	100	33.33	0	100	0
Tapirus bairdii	TBA	20	Bra	27.85	25.05	75	90	10	25	35	40
Cephalophus natalensis	NA	4	Bra	32	27	0	100	0	0	25	75
Browsers											
Boocercus euryceros	BE	15	Bra	6.77	5.13	13.33	53.33	0	100	0	0
Tragelaphus imberbis	TI	19	Bra	16.84	7.08	22.22	27.78	47.37	83.33	0	16.67
Giraffa camelopardalis	GC	28	Bra	5	8.66	54.17	20	0	91.67	0	8.33
Camelus bactrianus	CB	3	Hyp	79.83	9.17	100	66.67	66.67	33.33	33.33	33.33
Alces alces	AA	9	Bra	27.15	10	44.44	0	0	66.67	0	33.33
Litocranius walleri	LW	22	Bra	27.14	11.77	9.09	27.27	45.46	90.91	0	9.09
Tragelaphus strepsiceros	TT	11	Bra	20.09	12.59	18.18	63.64	36.36	90.91	9.09	9.09
Camelus dromedarius	CL	7	Hyp	54.07	13.93	57.14	42.86	42.86	42.86	14.29	42.86
Diceros bicornis	DB	11	Mes	8.5	14.27	95.24	0	0	85.71	9.52	4.76
Antilocapra americana	AM	44	Hyp	25.21	15.52	53.49	79.55	69.77	37.21	0	62.79
Seasonal-Regional Mixed											
Taurotragus oryx	TO	20	Mes	39.83	12.23	55	55	42.11	44.44	16.67	38.89
Budorcas taxicolor	BT	15	Hyp	7.97	13.73	33.33	56.25	0	100	0	0
Gazella granti	GG	41	Hyp	20.45	14.77	87.81	53.66	39.02	39.02	9.76	51.22
Tragelaphus scriptus	TS	31	Bra	19.08	15.87	19.36	19.36	22.58	70.97	16.13	12.9
Lama vicugna	VI	7	Hyp	30.43	16.21	28.57	57.14	85.71	28.57	42.86	28.57
Ovis canadensis	OC	19	Hyp	13.21	16.71	31.58	42.11	47.37	15.79	15.79	68.42
Lama glama	LG	6	Hyp	4.92	18.42	100	0	16.67	100	0	0
Gazella thomsoni	GT	23	Hyp	24.07	18.57	80.95	57.14	30.44	14.29	14.29	71.43
Capricornis sumatraensis	CA	11	Hyp	40.14	21.73	55.56	44.44	80	77.78	0	22.22
Boselaphus tragocamelus	TR	9	Mes	23.61	25.72	55.56	44.44	88.89	44.44	22.22	33.33
Axis axis	AX	43	Mes	13.56	28.28	75.61	9.76	9.76	52.5	22.5	25
Muntiacus muntjak	MM	10	Bra	20.45	18.95	80	72.73	30	20	0	80

TABLE 1
Continued

Taxon	Abbrev.	N	Hypso.[a]	Aver. pits	Aver. scratches	% Cross scratches	% Large pits	% Gouges	% Fine scratches	% Coarse scratches	% Mixed scratches
EXTANT SPECIES (*continued*)											
Meal by Meal Mixed											
Cervus unicolor	CU	11	Mes	21.27	26.27	100	36.36	100	18.18	45.46	36.36
Ovibos moschatus	OM	20	Hyp	28.45	29.68	15	100	85	50	0	50
Cervus canadensis	CC	28	Bra	18.64	30.63	96.43	42.86	21.43	82.14	0	17.86
Capra ibex	CI	9	Hyp	7.56	25.17	30	50	20	10	0	90
Grazers											
Connochaetes taurinus	CT	27	Hyp	4.93	20.61	44.44	40.74	7.41	44.44	7.41	48.15
Equus burchelli	EB	51	Hyp	11.52	21.72	60	48.98	50	40	10	50
Hippotragus niger	HN	5	Hyp	5.9	22.7	0	60	0	20	40	40
Bison bison	BB	18	Hyp	3.53	24.81	94.44	38.89	5.26	22.22	50	27.78
Tetracerus quadricornins	TQ	8	Mes	22.25	25.75	50	87.5	75	87.5	0	12.5
Equus grevyi	EG	11	Hyp	7.86	26.09	66.67	63.64	58.33	0	66.67	33.33
Kobus ellipsiprymnus	KE	14	Hyp	17.39	27.79	57.14	76.92	53.85	20	0	80
Alcelaphus buselaphus	AB	6	Hyp	13.58	29.58	12.5	75	62.5	0	12.5	87.5
Cervus duvauceli	CD	26	Mes	15.79	30.5	60	16	0	12	4	84
Suids											
Hylochoerus mainerdjag	HM	3		23.33	17	100	0	0	100	0	0
Potamochoerus porcus	PP	14		34.79	20.14	100	92.86	35.71	7.14	42.86	50
Elephants											
Loxodonta africana	LA	9	Hyp	15.94	24.5	100	100	100	0	100	0
Elephas maximus	EM	7	Hyp	9.86	28.14	85.71	71.43	85.71	0	71.43	28.57
FOSSIL EQUIDS											
Hyracotherium spp.	HYRACO	33	Bra	21.21	20.44	50	40.63	0	43.33	13.33	43.33
Mesohippus spp. mostly *bairdii*	MESO	29	Bra	19.79	32.62	22	2.78	3.03	93.94	0	6.06
Mesohippus westoni	MW	3	Bra	13.67	23.67	100	0	0	100	0	0
Mesohippus hypostylus	MH	5	Bra	12.13	34.63	100	0	0	100	0	0
Mesohippus-Miohippus	M-M	3	Bra	8.5	29.33	100	0	0	100	0	0
Parahippus spp.	P	10	Bra	12.81	28.77	90	0	0	77.78	11.11	11.11
Merychippus insignis	MERY	17	Mes	11.92	29.06	75	0	0	91.67	0	8.33
EXCLUDED SPECIES											
Capra hircus	CH	4	Hyp	21.17	16.33	50	0	25	75	0	25
Capreolus capreolus	OL	6	Bra	37.08	25.67	83.33	66.67	16.67	0	16.67	83.33

[a] Hypso., hypsodonty; Hyp, hypsodont; Mes, mesodont; Bra, brachydont.

transparency of the casts involved and the angle of incident light required to achieve good contrast. It is easier to set the light parameters at a low magnification (and find the most appropriate counting area at the same time) and then zoom up to 35× magnification. In addition, latex gloves do work well if light is allowed to shine through the index finger (held between the light source and the cast) while holding the cast. This simple action absorbs some of the intensity of the light beam before it strikes the specimen and always makes features stand out in relief. In the future, filters may achieve similar (but possibly not better) results. Fortunately, very few changes are required to achieve appropriate focusing and lighting conditions from specimen to specimen if they are approximately the same basic shape and size.

EXTANT SPECIES

Although there are detailed studies of the diet of individual species, the diet of numerous and varied species of ungulates has not been studied collectively by a single comprehensive study. Table 1 lists the new dietary classification. Several sources were used to compile this dietary classification: in particular, see Tener, 1965; Schaller, 1967; Hofmann and Stewart, 1972; Hofmann, 1973; Labâo-Tello and Van Gelder, 1975; Schaller, 1977; Sinclair, 1977; Bigalke, 1978; Kingdon, 1979; Gautier-Hion et al., 1980; Gauthier-Pilters and Dagg, 1981; McDonald, 1981; Chapman and Feldhammer, 1982; Lumpkin and Kranz, 1984; Kingdon, 1982a, 1982b; Nowak and Paradiso, 1983; Hofmann, 1985; Schaller et al., 1986; Janis, 1988; Feer, 1989; Hofmann, 1989; Nowak, 1991; Fortelius and Solounias; and Vrba and Schaller, 2000). Fortelius and Solounias (2000) provided a ‘‘conservative’’ classification where doubtful cases were treated as mixed feeders and a ‘‘radical’’ classification where microwear results separated certain mixed-feeder species into browsers and grazers. It is the ‘‘radical’’ classification of Fortelius and Solounias (2000) which was primarily used to establish our current dietary classification (table 1). In the present study two changes stand out: the duikers are separated from browsers as fruit and browser feeders (f-b) and the chital (*Axis axis*) is placed in the mixed-feeder category instead of in the grazing category. These changes do not alter the database in any major way, as duikers were recognized as distinct within the browsers by Fortelius and Solounias (2000) although they were for simplicity included in the browsers. In summary, species were subdivided into the following dietary categories: f-b, fruit and browsers (includes duikers and other similar species); b, browsers; g, grazers; and m, mixed feeders. The following species were treated separately because their microwear results were distinctive from other extants within their trophic group or because of distinctive or unusual dietary habits: duikers, tapirs, proboscideans, and suids.

MICROWEAR

Good photographs of microwear are difficult to obtain with the light microscope (fig. 2). Thus, SEM photographs are included in the present study to best show the various microwear features (figs. 3–7). The white rectangles of figure 2 show the area of a 500× SEM photograph as it appears at 35× magnification. Examining microwear features with the light microscope is easy and effective; photographing transparent casts at low magnification with a beam of light shining at a shallow angle across their surfaces is not.

Pits and scratches were identified and counted within a standard 0.4 mm × 0.4 mm square area. Two representative enamel locations on the second band of enamel of the paracone (the crest adjacent to the central cavity as opposed to the most buccal band) were counted to standardize the methodology. This procedure is used because microwear is somewhat variable on a single tooth (personal obs.); the protocone represents the most scarred area, and the external bands of the paracone and metacone represent the least scarred area. The selected second band used here is intermediate in terms of the amount of wear observed. The second band was selected for selenodont ruminant artiodactyls and advanced equids (fig. 1A). However, in some perissodactyls (e.g., in tapirs, rhinoceroses, and *Hyracotherium*) a band

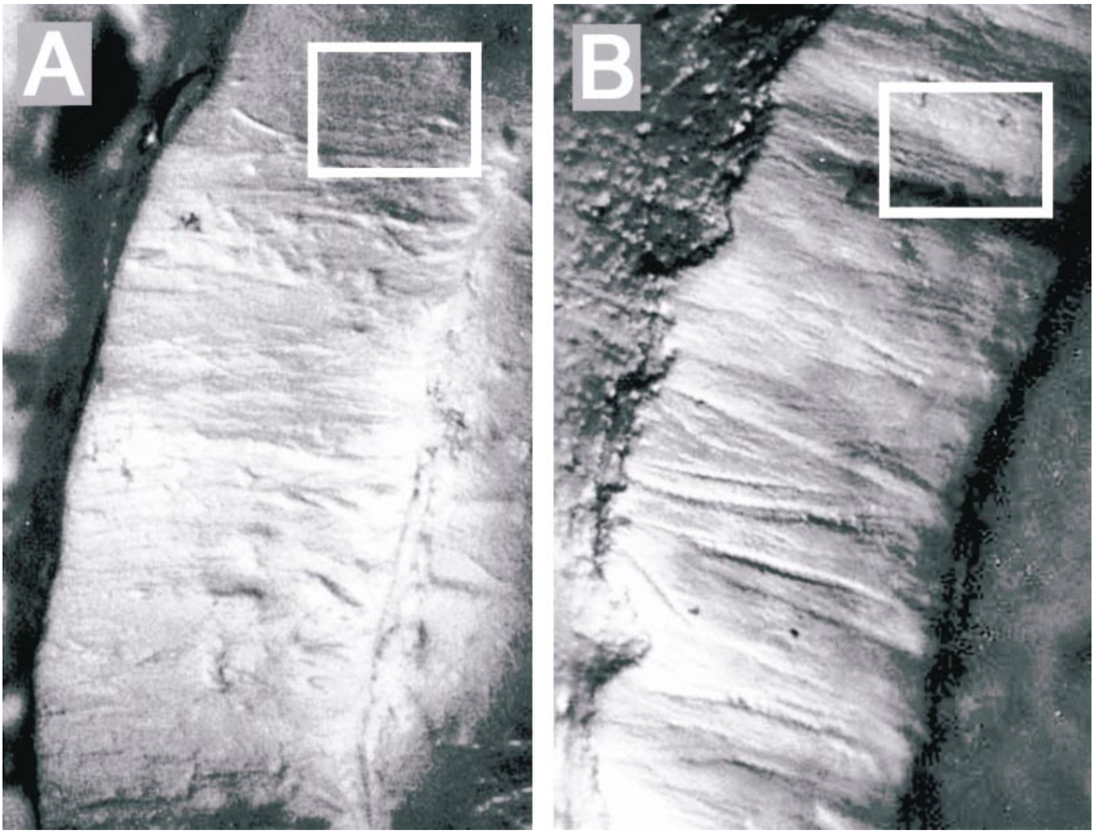

Fig. 2. Light microscopy of clear epoxy molds of zebra teeth at 35×. Bright areas result from reflections of the table below clear epoxy cast of tooth. White rectangles showing the size of a typical 500× SEM photograph in relation to the low magnification image.

was selected which was similar in position to that of the second band of ruminants. In suids (bunodont dentition), a medial region of the tooth was selected. In proboscideans, an area in the center of the molar (at the center of one of the lophs) was selected.

The absolute number of pits versus scratches for individuals per taxon was recorded in two locations on the same enamel band for both extant and fossil taxa. The two counts per paracone (per individual cast) were then averaged to obtain a mean number of pits and scratches per cast. These means were then averaged for all individuals per taxon to obtain a final average number of pits and scratches per taxon. Bivariate plots of these average numbers of pits versus scratches were constructed for extant ungulates. Mean numbers of pits and mean numbers of scratches were calculated for all taxa comprising each dietary category to obtain a mean value and ranges for browsing, grazing, and mixed feeding ungulates.

New microwear characters were developed and scored with the intent of providing a mechanism to further refine the dietary categorization of ungulates beyond the broad categories of browser versus grazer versus mixed feeder. Thus, the quantity of large versus small pits was also scored by noting if more than four large pits were present or absent per microscope field. Most pits observed in dental enamel are what are here called ‘‘small’’. They are very regular in appearance with sharp, distinct borders, being circular in nature and very refractive or shiny (and bright). Actual pit diameters were not quantified; instead, differences in diameter were qualitatively ranked as small (i.e., the most numerous type observed) or large (rel-

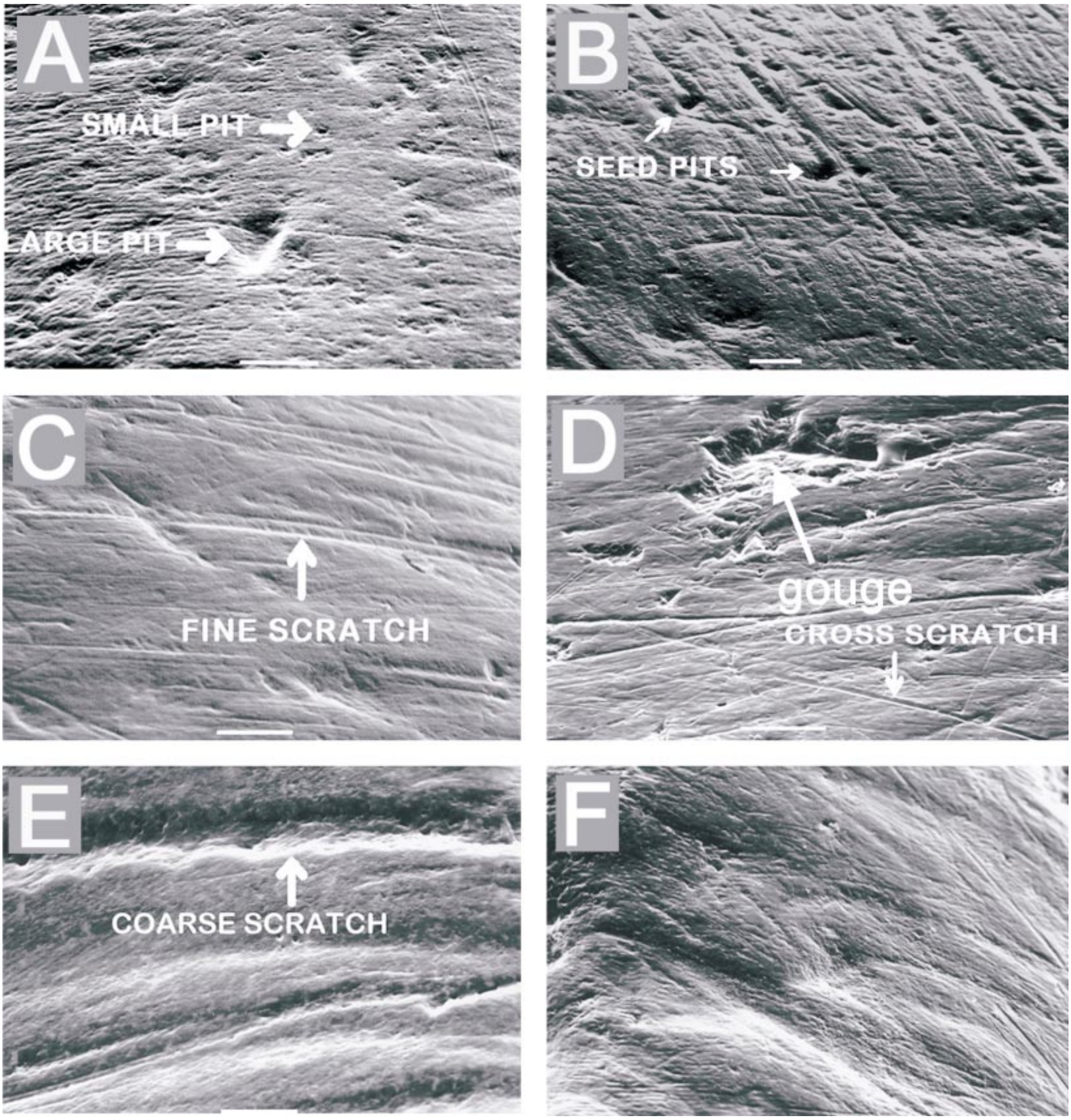

Fig. 3. SEM photomicrographs at 500×. **A:** Surface showing small and large pits; *Tragelaphus scriptus*. **B:** Large puncturelike pits thought to result from seeds; *Tapirus terrestris*. **C:** Mostly finely scratched surface; *Bison bison*. **D:** Surface showing a gouge and cross scratches; *Ovis canadensis*. **E:** Coarse scratch and fine scratches; *Bison bison*. **F:** Mixture of scratches; *Gazella granti*. Note microwear scratch textural diversity in the two images from *Bison*.

atively few in number). The differences in pit diameters are immediately obvious at 35× magnification and are easy to discern. Some enamel bands have pits that are considerably larger than the typical and more numerous type; they are here called ‘‘large’’. These large pits are deeper, less refractive (always dark), generally at least about twice the diameter of small pits, and often have less regular outlines than do small pits but are still generally circular. Some large pits are very deep and puncturelike with relatively sharp edges. Figure 3A shows small and large pits.

Scratches on each tooth (e.g., figs. 2–7)

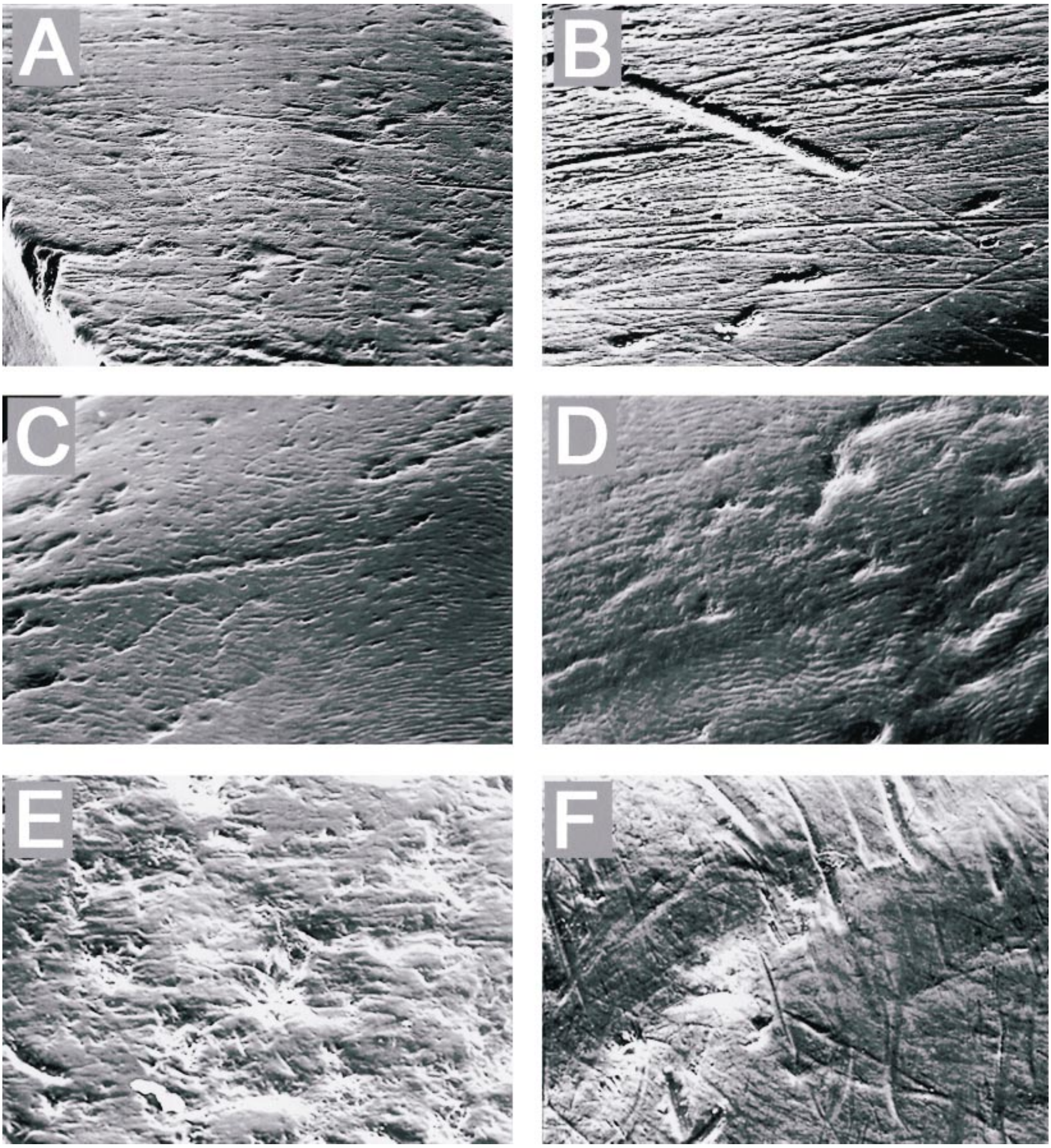

Fig. 4. SEM photomicrographs at 150–200×. **A:** *Tragulus javanicus*; surface showing small pits. **B:** *Tapirus bairdii*; surface showing coarse scratches and a hypercoarse cross scratch probably due to hard fruit and or seed coverings. **C, D:** *Tragelaphus imberbis*; mostly unscratched surface. Small pits are discernible. Enamel prisms are discernible as wavy lines on a polished surface. **E, F:** *Potamochoerus porcus*; numerous large pits and gouges and wide scratches are visible. Note that these images are of lower magnification than figures 5–7. Courtesy of A. Walker.

were also qualitatively scored. Each tooth was scored in terms of being comprised of either purely coarse scratches, purely fine scratches, or a mixture of both types of textures per tooth surface. Scratch widths were not quantified, but were qualitatively scored based on general appearance (e.g., figs. 3C, E, 5A, B, and 7). Quantifying the width of scratches would prove very time- consuming, and defeat the purpose of using a rela-

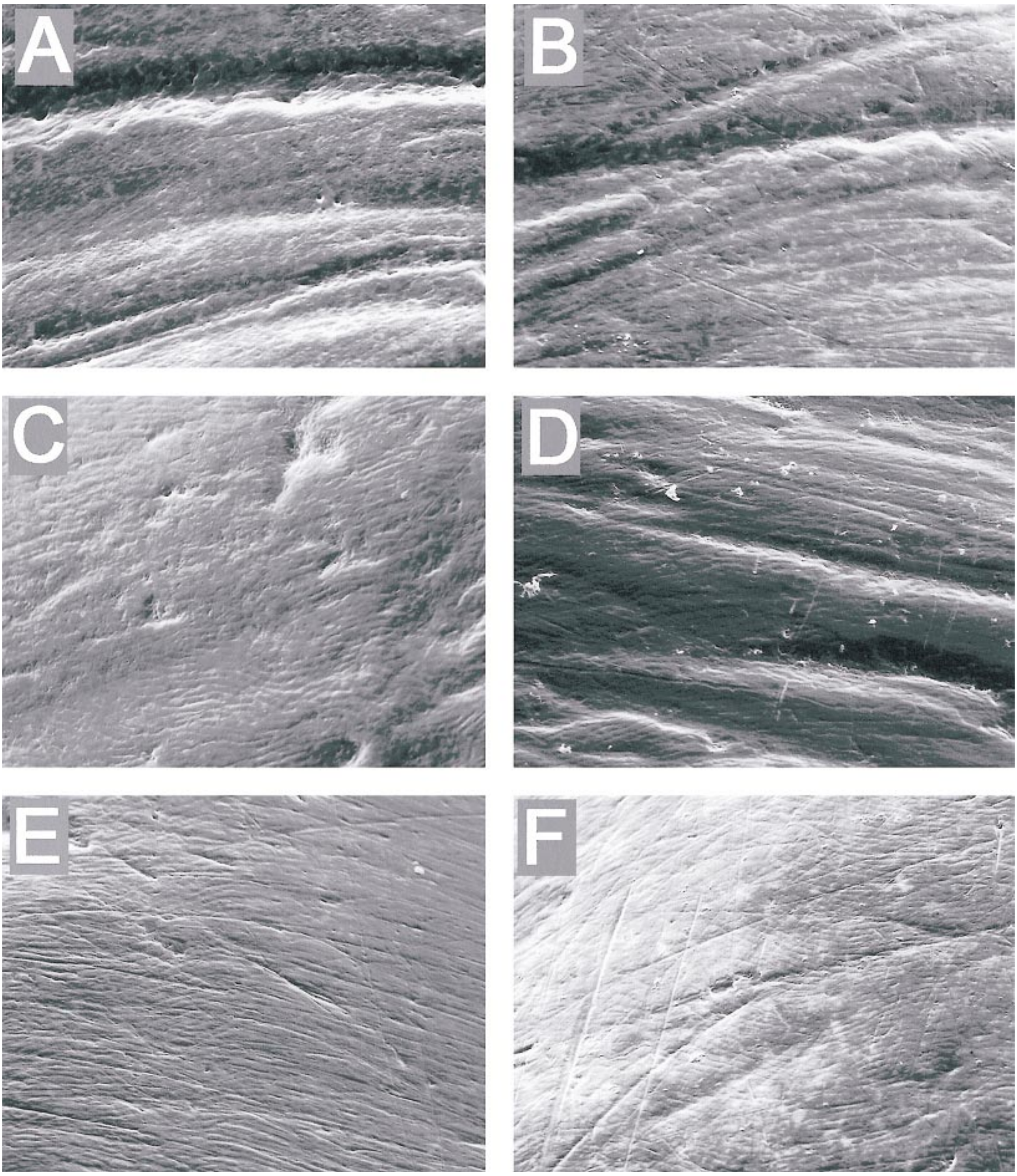

Fig. 5. SEM photomicrographs at 500×. **A, B:** *Syncerus caffer*; wide coarse scratches, polished surfaces, and fine scratches. **C:** *Tragelaphus scriptus*; enamel prisms on polished surfaces and a few pits. **D:** *Kobus ellipsiprymnus;* prisms polished surfaces and wide scratches. **E:** *Tragelaphus scriptus*; enamel prisms on polished surfaces and fine scratches. **F:** *Taurotragus oryx*; many fine cross scratches on a polished surface with enamel prisms showing through.

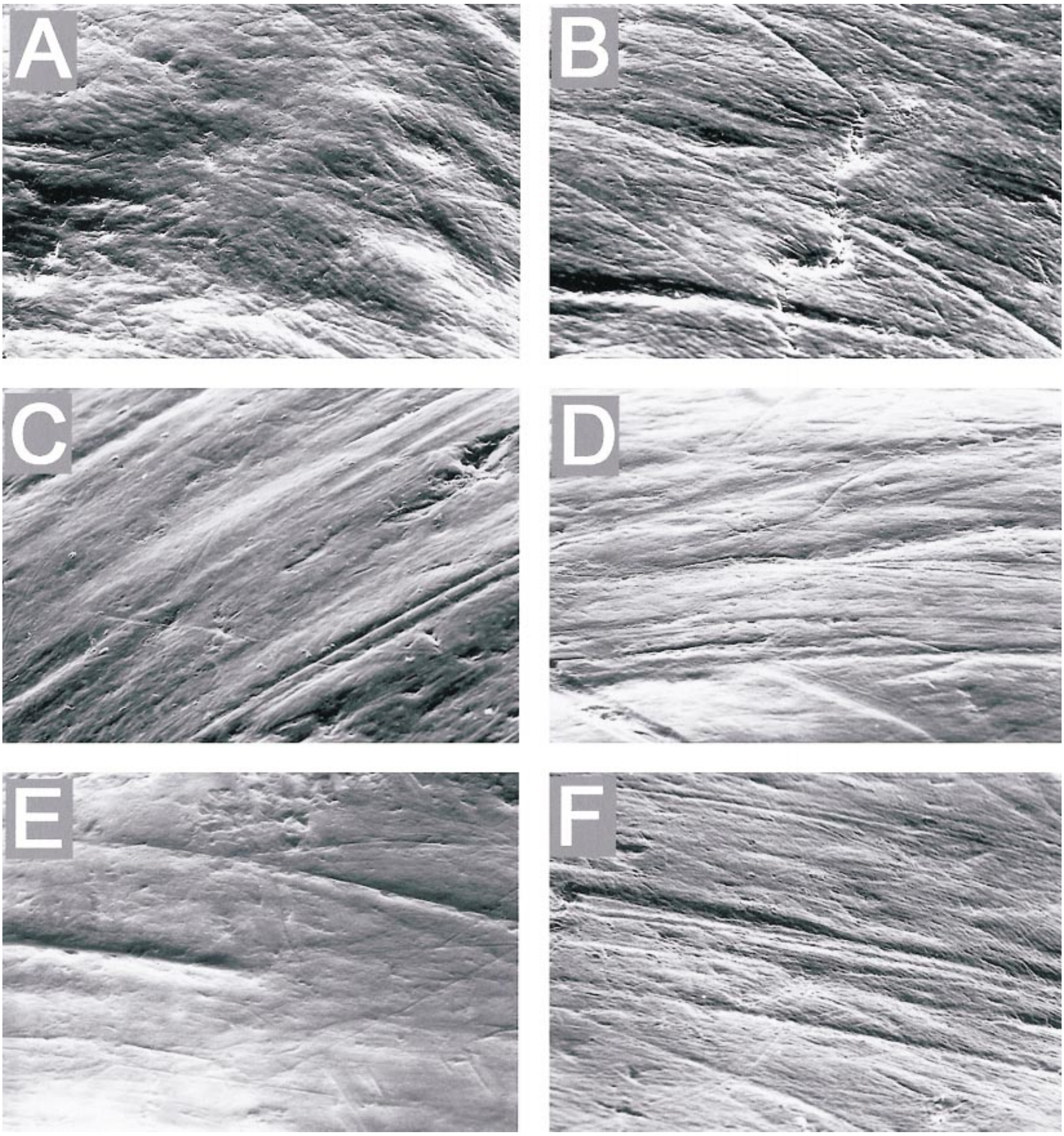

Fig. 6. SEM photomicrographs at 500×. **A, B:** *Gazella granti*; fine scratches, cross scratches, and polished surfaces. **C, D:** *Connochaetes taurinus*; typical grass scratches (mixed fine and coarse) and an abraded surface where a few prisms are visible. **E:** *Connochaetes taurinus*; numerous pits and cross scratches of various widths and an abraded surface where a few prisms are visible. **F:** *Bison bison*; many fine and coarse scratches and a few pits on polished surface where prisms are visible.

tively easy and fast methodology for the attainment of large sample sizes. ‘‘Fine’’ scratches are defined as those scratches that appear the narrowest (fig. 7). Fine scratches are relatively shallow and have lower refractivity (are duller) than do coarse scratches. ‘‘Coarse’’ scratches are defined as those scratches that appear the widest (fig. 5A, B). Coarse scratches are also relatively deep and have high refractivity (relatively shiny). The ‘‘mixed’’ scratch category is based on the finding of a high percentage of both fine and

TABLE 2

Distribution of Extant and Extinct Species on the Basis of Scratch Counts and Types of Diet[a]

Traditional browsers		The browsing-grazing transitional phase						Traditional grazers	
Scratch range 0–17		Scratch range 0–17 Scratch range 17.5–29.5		Scratch range 0–17 Scratch range 17.5–29.5 As well as 30 and greater		Scratch range 17.5–29.5 As well as 30 and greater		Scratch range 17.5–29.5	
Hypso.&SW[b]	Species[c]	Hypso.&SW[b]	Species[c]	Hypso.&SW[b]	Species[c]	Hypso.&SW[b]	Species[c]	Hypso.&SW[b]	Species[c]
Browsers, fruit dominated		**Browsers, fruit dominated**		**Browsers, fruit dominated**		**Browsers, fruit dominated**			
				Bra c	*Okapia johnstoni* (OJ) 1				
Bra m	*Cephalophus niger* (NI) 1	Bra c	*Cephalophus dorsalis* (DR) 1	Bra m	*Cephalophus silvicultor* (SL)	Bra m	*Cephalophus natalensis* (NA)		
		Bra m-3	*Tapirus terrestris* (TRR) 1	Bra m-3	*Muntiacus muntjak* (MM)				
				Bra m-3	*Tapirus bairdii* (TBA) 1				
				Bra c	*Tragulus* spp. (TRA)				
				Bra c	*Moschus moschiferus* (MO)				
Browsers, leaf dominated		**Browsers, leaf dominated**							
Bra f	*Giraffa camelopardalis* (GC)								
Bra f	*Alces alces* (AA) 1	Bra f	*Litocranius walleri* (LW) 1						
Bra f+	*Boocercus euryceros* (BE)								
Mes f	*Diceros bicornis* (DB) 1	Bra f	*Tragelaphus imberbis* (TI)						
		Bra f	*Tragelaphus strepsiceros* (TT)						
Hyp f-m	*Camelus bactrianus* (CB)	Hyp f-m	*Camelus dromedarius* (CL)						
		Hyp m	*Antilocapra americana* (AM)						
		Seasonal-regional mixed feeders		**Seasonal-regional mixed feeders**		**Meal by meal mixed feeders**			
		Bra f	*Tragelaphus scriptus* (TS) 1	Hyp f	*Capricornis sumatraensis* (CA)	Bra f	*Cervus canadensis* (CC)		
		Hyp f+	*Lama glama* (LG)	Hyp f+	*Budorcas taxicolor* (BT)				
		Hyp f	*Capra hircus* (CH)						
		Mes m	*Taurotragus oryx* (TO)	Mes m	*Axis axis* (AX)	Mes m	*Cervus unicolor* (CU) 1		
		Hyp m	*Gazella granti* (GG)	Mes m	*Boselaphus tragocamelus* (TR)	Hyp m	*Ovibos moschatus* (OM) 1		
		Hyp m	*Gazella thomsoni* (GT) 1						
		Hyp m	*Lama vicugna* (VI)						
		Hyp m	*Ovis canadensis* (OC)						
						Hyp m-3	*Capra ibex* (CI)		

TABLE 2
Continued

Traditional browsers		The browsing-grazing transitional phase						Traditional grazers	
Scratch range 0–17		Scratch range 0–17 Scratch range 17.5–29.5		Scratch range 0–17 Scratch range 17.5–29.5 As well as 30 and greater		Scratch range 17.5–29.5 As well as 30 and greater		Scratch range 17.5–29.5	
Hypso.&SW[b]	Species[c]	Hypso.&SW[b]	Species[c]	Hypso.&SW[b]	Species[c]	Hypso.&SW[b]	Species[c]	Hypso.&SW[b]	Species[c]
					Grazers		**Grazers**		**Grazers**
						Mes f	*Tetracerus quadricornis* (TQ)		
				Hyp m	*Connochaetes taurinus* (CT) 1	Hyp m	*Kobus ellipsiprymnus* (KE)	Hyp c-m	*Hippotragus niger* (HN)
						Hyp c-m	*Equus grevyi* (EG)	Hyp m	*Equus burchelli* (EB) 2
				Hyp m-3	*Alcelaphus buselaphus* (AB)				
				Mes m-3	*Cervus duvauceli* (CD)				
				Bra m-3	*Capreolus capreolus* (OL)				
								Hyp c-m	*Bison bison* (BB) 3
			Suids		**Proboscidean**		**Proboscidean**		
		f+	*Hylochoerus meinertzhageni* (HM)						
		m	*Potamochoerus porcus* (PO) 1			h	*Elephas maximus* (EM)		
				h	*Loxodonta africana* (LA)				
					Extinct equids				
				Bra f	*Mesohippus westoni*	Bra f	*Mesohippus bairdii* and spp.		
						Bra f	*Mesohippus-Miohippus* (larger than *M. bairdii*)		
						Bra f	*Parahippus nebrascensis*		
						Bra f	*Parahippus cognatus*		
						Mes f	*Merychippus insignis*		
						Bra f+	*Mesohippus hypostylus* (only high scratch)		
				Bra m	*Hyracotherium* spp.				

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[a] For a detailed discussion of this table, see "Deriving Table 2" in the text.

[b] Hypso.&SW, hypsodonty and scratch width; Hyp, hypsodont; Mes, mesodont; Bra, brachydont; f, fine; c, coarse, m, mixed widths; h, hypercoarse scratches; f+, fine scratches only.

[c] Species abbreviations (in parentheses) are included. Numbers following some species names indicate number of individuals omitted.

Fig. 7. *Cervus canadensis* at 500×; an overscratched surface where new scratches would fall upon preexisting ones.

coarsely textured scratches in the same enamel band.

The presence or absence of more than four cross scratches per microscope field was also recorded. Cross scratches have been noted in prior microwear studies and are defined here similarly as those scratches which are oriented somewhat perpendicularly to the majority of scratches observed on dental enamel (fig. 3D, F).

Some enamel bands show microwear scars that are quite distinct from pits but are still fairly circular when located within the enamel band proper. These features are here called ‘‘gouges’’. Gouges in enamel are rarer than pits but are very distinctive when present (fig. 3D). They have ragged, irregular edges and are much larger (approximately 2–3 times as large) and deeper than large pits. They are relatively dark features with low refractivity and are most often observed on the edges of the buccal side of the second enamel band (enamel band one and four shows little gouging). The presence or absence of gouges in a microscope field was recorded.

Data from each individual tooth therefore consisted of the following variables: average number of pits, average number of scratches, percentage of individuals per taxon displaying more than four large pits per field, percentage of individuals with more than four cross scratches per field, percentage of individuals per taxon with fine versus coarse versus a mixture of fine and coarse scratches, and percentage of individuals per taxon with gouges present.

A large sample of fossil equids from the American Museum of Natural History were analyzed with the new method of microwear. Members of the North American genera *Hyracotherium*, *Mesohippus*, *Parahippus*, and *Merychippus* were compared to the new comparative extant ungulate microwear morphospace for dietary interpretation. Taxa included here span the presumed browsing to grazing transition in the fossil record of the North American Equidae.

DERIVING TABLE 1: Table 1 summarizes the tooth microwear results (quantitative and qualitative) obtained on the extant and the extinct species used in this study. The quantitative results list the average number of pits and scratches per taxon. The qualitative results (presence or absence of features) include the percentages of specimens per taxon with finely textured, coarsely textured, or a mixed realm of scratches (fine and coarsely textured), as well as the percentages of specimens per taxon with large pits (more than four), cross scratches (more than four), and gouges. Within the table, the species are sorted by dietary category and by increasing number of scratches.

DERIVING TABLE 2: It is elucidating to further sort extant species along a dietary axis based on the spread of scratch numbers observed in a particular taxon. This process highlights differences in extant species' diets and provides a more precise understanding of the diet of both extant and extinct forms. At 35× magnification, a 0.4-mm-square surface of enamel can have no scratches or as many as 130 in some cases (both of these extremes are rare however). The counted scratches of each species form a distribution. For example, the scratch counts for *Budorcas taxicolor* range from 0 to 36, while those for *Axis axis* range from 2.5 to 51.5.

The ranges of scratches for each column in table 2 were initially established on the basis of results obtained for typical browser and typical grazer species (e.g., giraffe or bison, respectively); that is, we used well-known and typical species to determine the means and ranges which defined each dietary category. The average scratch versus pit results are shown in figure 8; the patterns are similar to previously published microwear at higher magnifications (Solounias and Moelleken, 1992a, 1992b, 1993a, 1993b, 1994).

To construct the columns in table 2, raw scratch ranges for well-known browsers (0–17) and grazers (17.5–29.5) were used to establish two of the three scratch ranges that characterize each species. The third range (30 or greater) was established after observing that some species contained individuals that possessed more scratches than do typical grazers. Therefore, to assess the scratches for each species, raw scratch counts were subdivided into a low count range (from 0 to 17 scratches), a medium count range (17.5–29.5), and a high count range (30 scratches and greater). Decimals (e.g., results such as 29.5) result from the averaging of two separate counts of scratches per tooth. What are here termed ‘‘traditional browsers’’ have individual scratch counts from 0 to 17; ‘‘traditional grazers’’ from 17.5 to 29.5. The species are sorted into one of five categories in table 2 according to the type of scratch distributions they possess: namely into species that have scratch counts which range only from 0 to17 scratches per tooth (first column), being the traditional browsers; species that have scratches which range between 0 and 17 and between 17.5 and 29.5 (second column); species that have scratches in three ranges: 0–17, 17.5–29.5, and 30 and greater (third column); species that range between 17 and 29.5, and those with 30 and greater (fourth column); and species that have only between 17.5 and 29.5 (fifth column), being traditional grazers. The meaning of these five subdivisions will be explained in the Results and Discussion sections. Within each of these five columns, species are further sorted (vertically) according to their respective dietary categories into fruit and browser feeders (duikers and certain primitive ungulates); leaf-dominated browsers, grazers, mixed feeders, proboscidea, and suids.

When partitioning species into the scratch range columns shown in table 2, we observed that many species fell into unexpected categories. For example, in *Okapia johnstoni* (a browser), approximately half of the individuals sampled have scratch counts from 17.5 to 29.5. This deviation from other browsers could not be ignored. Thus, the okapi could not be placed with species such as *Giraffa camelopardalis* and *Boocercus euryceros*, but rather in a new category of browsers. This sorting process produces the five columns that represent five combinations of scratch counts.

Finally, clarification is necessary about deriving table 2. Ideally, if numerous specimens are examined, species may have similar apparent scratch ranges due to the presence of one or two extreme outliers. This is because animals feed on a variety of plant foods, some of which are atypical. Thus, it is possible with a very large sample to pick up the extremes (i.e., teeth with no scratches, as well as teeth with very numerous or supernumerary scratches) for many species. These outliers affect the apparent range of scratches observed (i.e., broaden it), and the scratch pattern represented by the vast majority of teeth is obscured.

To differentiate a clear and more representative scratch pattern, certain teeth must be overlooked. Thus, *Diceros bicornis* has a range from 10 to 16.5 but one tooth has 19 scratches. We place this species in the same column with *Giraffa camelopardalis* and *Boocercus euryceros* and consider this one tooth out of range. These slight adjustments were necessary to more accurately represent the majority of scratch results actually present in a species. This adjustment was done for the traditional grazers as well. In table 2, the number next to a species indicates how many outliers were excluded from the sample.

STEP-BY-STEP SUMMARY OF NEW MICROWEAR TECHNIQUE: Select a sample of specimens from adult individuals. Remove any museum shellac or hardeners that might be present on the tooth surfaces by applying Zip Strip to the surfaces of each tooth with a cotton swab. Latex gloves should be used throughout the molding process. After 30 minutes, lightly scrub the surfaces with more Zip Strip. With 95% alcohol and cotton balls, remove Zip Strip and wipe clean several times. Lightly scrub the enamel surface with alcohol once again, but this time with cotton swabs to ensure that enamel bands are adequately cleaned. Let teeth dry well. Apply small amounts of molding compound with an applicator gun. Initially, only enough molding material is applied to just cover the tooth surface. This is because the first mold is applied as a cleaning step and then allowed to set until hardened. The first mold is removed and discarded and molding compound is applied once again but this time the entire tooth surface is molded, including the application of molding compound to the buccal and lingual surfaces of the tooth. Applying some molding material to these surfaces ensures the presence of lateral walls in the mold, which facilitates the process of making epoxy casts. Remove final molds after they harden and trim any extraneous molding material around the edges of each mold. Using lab putty, make retaining walls around the edges of each mold. It is important to make sure that the putty adheres well to the mold to avoid leaks when casting and that the mold can be set horizontally onto the table. Mix epoxy and hardener well and stir with a tongue depressor. The mixture will be full of bubbles if stirred well. After mixing, pour into test tubes and centrifuge well at a low speed for 4–6 minutes. The mixture should be now free of bubbles except for a small amount of froth on the surface. Pour the centrifuged epoxy into each mold slowly from the edge of the mold so that the epoxy fills in the depressed areas of the mold gradually to minimize bubbles. Fill the mold so that epoxy is near the top of the putty-retaining wall. Let the mold-cast specimens harden for 1–2 days before removing the casts. Hold casts under the microscope so that the light source strikes the surface at a shallow angle. Adjust the position of the cast until the particular feature that you want to assess stands out in bold contrast. Reposition the angle that the cast is held to best visualize the next feature until all microwear scars are viewed and scored. Slight position adjustments of the cast are necessary to modify the angle of the incident light beam. This adjustment is necessary because different features have different dimensions and depths, and therefore, refract light slightly differently from each other.

RESULTS

EXTANT SPECIES

The new microwear results correlate well with the broad dietary assignations previously given to extant species, their actual diets observed in the wild, and with the results obtained with the 500× higher scanning electron microscope magnifications. However, additional dietary patterns and some interesting discrepancies were obtained and are explained below.

NUMBER OF PITS AND SCRATCHES: AVERAGES AND RANGES (QUANTITATIVE)**:** Scratches are more discriminating than pits. This is because there is no overlap in the scratch averages between browsers and grazers (fig. 8A). Table 2 separates the species according to an increasing number of scratches (from left to right), except for column 5, which has less scratches than does column 4 (an explanation follows). The range of individual scratch counts of traditional browsers is from 0 to17 and that of the traditional grazers from 17.5 to 29.5. Although the scratch averages are distinct between browsers and grazers, individual raw scratch counts may overlap (table 1). Traditional species are listed in columns 1 and 5 of table 2. They are termed traditional because the browsers have homogeneous low-scratch results and the grazers have homogeneous high-scratch results, mirroring results obtained in past microwear studies. Columns 2, 3, and 4 of table 2 are termed ‘‘the browsing-grazing transitional phase’’ (the taxa found here are represented in fig. 8A). Taxa in column 2 are browsers with scratch ranges between 0 and 17 and between 17.5 and 29.5; taxa in column 4 are grazers with scratches falling between 17.5 and 29.5 and also greater than 30. These browsers and grazers (listed in columns 2 and 4 of table 2) overlap in the scratch range of 17.5–29.5. Although the microwear of the browsers of column 2 is different from that of the traditional browsers (column 1), we retain their diet as a type of browsing. Grazers in column 4 differ from the traditional grazers of column 5 by having some scratches, which fall in the range of 30 and above. Taxa placed in column 3 include browsers and grazers that have the broadest range of scratches (i.e., broken into three ranges of

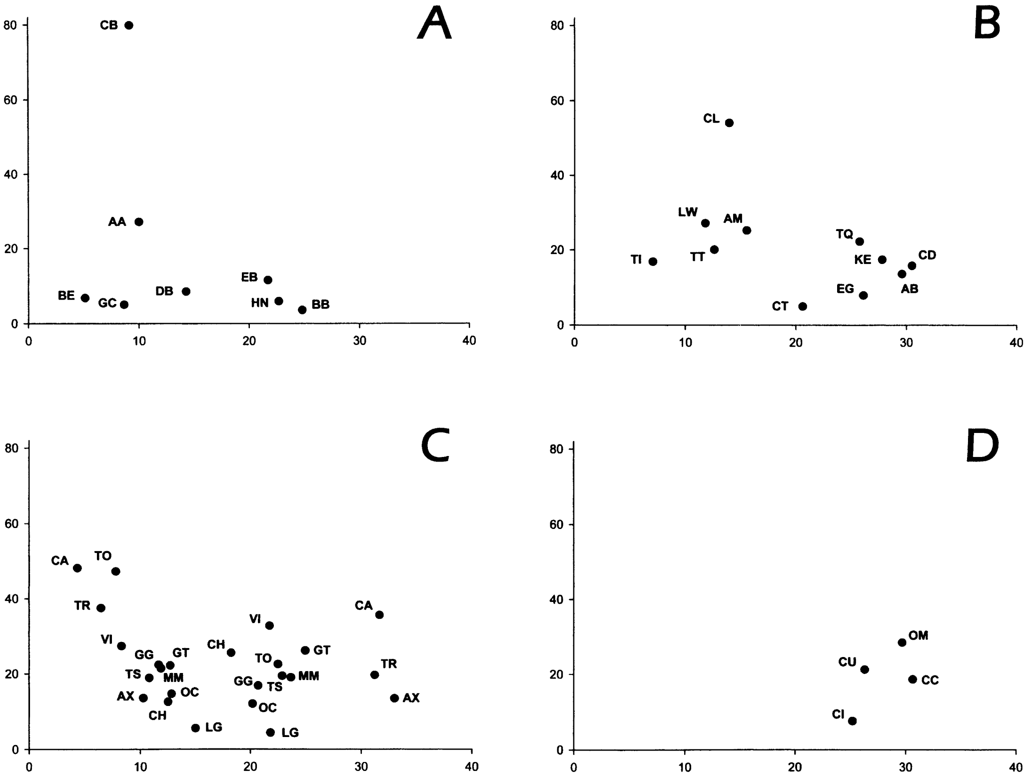

Fig. 8. Average number of pits (y axis) versus average number of scratches (x axis) for extant species. **A:** Traditional extant browsers and grazers. The gap between browsers and grazers is clearly seen. **B:** Browsers and grazers within the browsing-grazing transitional phase. **C:** Plot of extant seasonal mixed feeders that have been subdivided into two means: one for browsing to the left and another for grazing to the right. **D:** The nonseasonal mixed feeders cannot be subdivided and are plotted as a single point.

scratch counts: 0–17; 17.5–29.5, and 30 and greater). Despite the wide range of individual scratch counts, the average scratch numbers of these species still plot within the appropriate boundaries of their respective dietary group. That is, the browsers plot with the browsers and the grazers with the grazers (fig. 8B).

The average number of pits overlap between browsers and grazers, especially at the low range (less than 20 pits). Only browsers, however, have taxa with more than 40 pits on average. This is most noticeably due to the very high average pit numbers observed in camels (fig. 8B). Therefore, the average pit number alone should not be relied on to discriminate browsing from grazing ungulates.

Figure 9 shows the average scratch and pit morphospace boundaries of all browsers and grazers as well as the distinctive gap between these two dietary groups. Grazers cluster in the high-scratch morphospace, and browsers cluster in the low-scratch morphospace. When the results for mixed feeders are averaged for each taxon (single average), species cluster mostly in the gap between browsers and grazers (fig. 9), although browse-dominated mixed feeders plot within the browsing morphospace and grass-dominated mixed feeders plot within the grazing morphospace.

UNDERCOUNTING OF SCRATCHES IN TAXA IN COLUMN 5 OF TABLE 2: It is probable that the most scratched teeth are those of the grazers in column 5 (table 2). The results are organized, however, such that columns 3 and 4 list species with higher counts (range 30 and greater) than those of column 5. This is be-

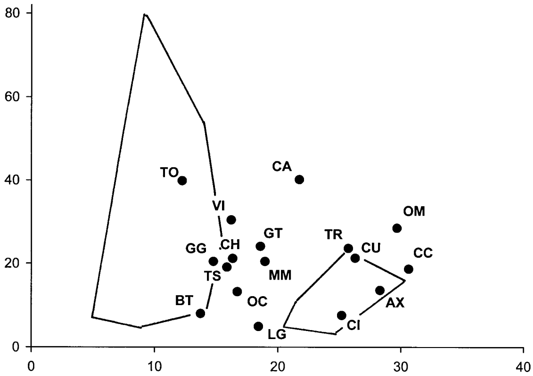

Fig. 9. Single means of mixed feeders fall mostly in the gap between browsers and grazers. The morphospace envelopes are those of all browsers and grazers (i.e., fig. 8A and B combined).

cause it is most likely that the scratch counts of species listed in column 5 are in fact underestimated. Phytoliths of grasses heavily scratch teeth, and thus scratches often fall on other preexisting scratches. A strongly scratched tooth may indeed appear less scratched in terms of countable scratches than one with fewer scratches. One explanation is that polished enamel surfaces create a clear mirrorlike scratch-free background where scratches are highly visible. The species in columns 1 through 4 have more polished dentitions due to lower abrasion and higher attrition. The polished background (due to more tooth-on-tooth contact) makes scratches appear more distinctive (i.e., scratches are distinctively spaced out with nonscratched enamel surface visible between them). Species in column 5 display a rough, totally scratched surface (due to more abrasive wear and tougher foods) where a background free of scratches is not visible and the enamel background is not polished. Thus, species with scratch numbers that range between 17 and 29.5 scratches (as in column 5) in reality possess more scratches than it may be possible to distinguish.

SEASONAL AND REGIONAL MIXED FEEDERS: All mixed feeders fall within the browsing-grazing transitional phase based on their raw scratch distributions (table 2). We distinguish two types of mixed feeders. When the average number of scratches versus pits is plotted, typical mixed feeders (seasonal or regional variation in diet) show samples with averages which cluster into the browsing and the grazing domains (as in fig. 8C; see also fig. 10). Such mixed feeders show two distinct forms of microwear within a particular species—one typical of browsing ungulates, and one typical of grazing ungulates. Figure 10A shows the distribution of actual raw scratch counts in a typical browser; figure 10B for a typical grazer (*Giraffa camelopardalis* and *Kobus ellipsiprymnus*, respectively). Figure 10C shows the raw scratch pattern for standard seasonal or regional mixed feeding taxa (e.g., *Gazella thomsoni*) where two scratch subsets are observed (a browsing type and a grazing type) within a single species. Most mixed feeding ungulates studied fall into such a bimodal pattern (fig. 8C; Solounias and Moelleken, 1994).

MIXED FEEDERS VARYING THEIR DIET ON A MEAL-TO-MEAL BASIS: Some mixed feeders have microwear that does not break up bimodally into two raw scratch subsets (browsing and grazing). Figure 8D graphs the average number of pits versus scratches for mixed feeder species that show only one type of microwear. These mixed feeders most likely vary their diets on a meal-to-meal basis rather than regionally or seasonally (Solounias et al., 2000a).

The mixed feeders are shown in table 2 sequestered into their respective columns (2, 3, and 4) according to their raw scratch distributions. No mixed feeders occur in columns 1 or 5 where the traditional browsers and grazers fall. This demonstrates that traditional browsers and grazers can be distinguished from mixed feeders by their scratch range distributions. The distinction of mixed feeders from the other browsers and grazers (from columns 2, 3, and 4) cannot be made using the scratch range partitioning shown in table 2. However, individual taxon scratch averages can be used to distinguish seasonal and regional mixed feeders (from columns 2 and 3) from browsers and grazers. Interestingly, the individual scratch range results of mixed feeders varying their diet on a meal-to-meal basis fall in column 4 and are therefore closest to results of traditional grazers.

OTHER EXTANT UNGULATES

Figure 11 shows the average number of pits versus scratches for the remaining un-

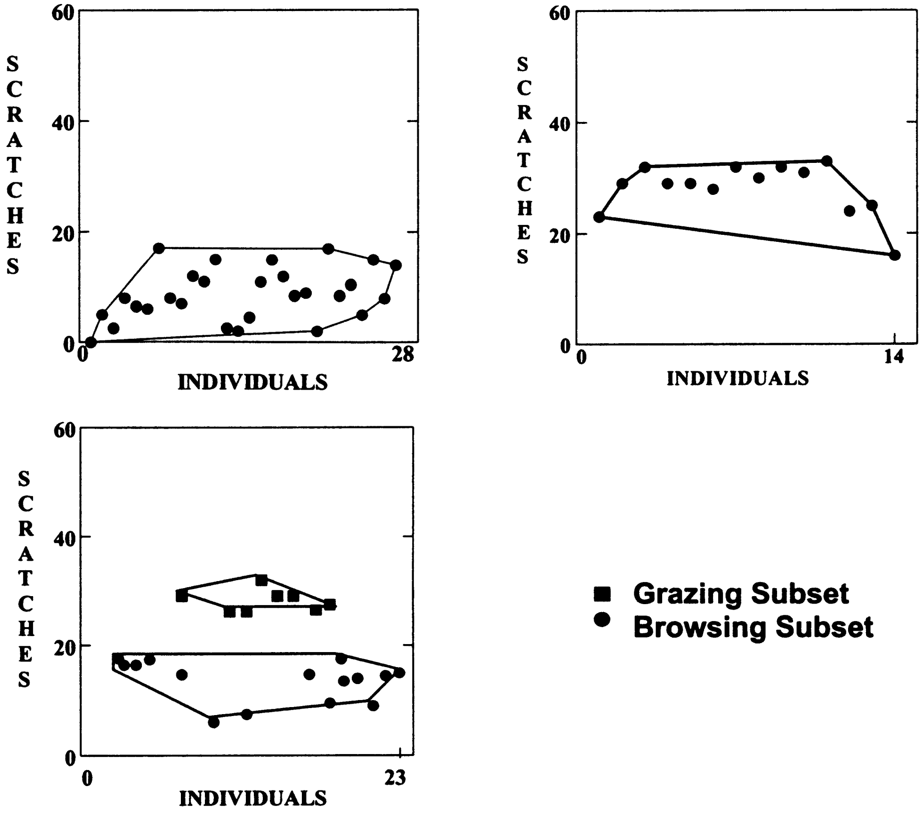

Fig. 10. Plots of individual tooth counts for a browser **(A),** grazer **(B),** and mixed feeder **(C)** (*Giraffa camelopardalis,* giraffe; *Kobus ellipsiprymnus,* common waterbuck; *Gazella thomsoni,* Thomson's gazelle) to show the similarity between the mixed feeder data to data resulting for a combination of a browser and a grazer.

gulate species examined, namely the duikers (*Cephalophus*), *Tragulus, Moschus,* suids, tapirs, and proboscideans. In figure 11A, species are plotted against the scratch and pit morphospaces of browsers and grazers. Figure 11B shows the tapirs and proboscideans plotted against the morphospace of browsers and grazers. This morphospace is basically a broad browsing and grazing domain, and as such is useful in comparisons of species which are poorly known in terms of microwear. The morphospace of traditional browsers and grazers is shown in figure 11A.

Duikers have heterogeneous results. For example, the average number of scratches in duikers ranges from low scratch averages in *Cephalophus niger* to high averages in *Cephalophus natalensis* (table 2; columns 1 and 4, respectively). *Cephalophus niger* falls within the traditional browsing scratch and pit morphospace; the other duikers fall into the gap between browsers and grazers (e.g., *C. dorsalis* and *C. silvicultor*) or they have scratch numbers more similar to extant grazers (e.g., *C. natalensis*). With the exception of *Cephalophus niger,* the duikers fall within the browsing-grazing transitional phase when scratch range distributions are considered. Thus, most of the duikers studied here, although browsers, fall within the mixed feeding and/or the grazing domain. Even so, the average number of pits is higher in duikers than in traditional grazers (fig. 11A).

Some of the high scratch numbers and /or high percentage of coarsely textured scratches found in duikers most likely result from their having consumed hard fruit and/or seed covers which may scratch teeth in ways sim-

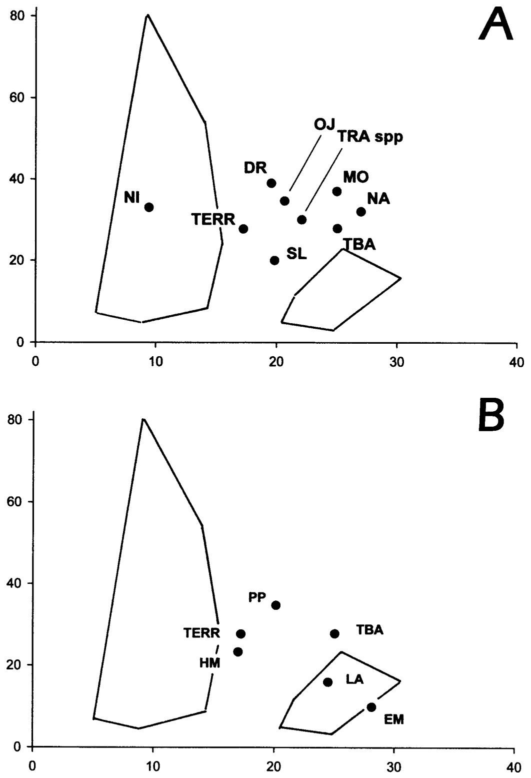

Fig. 11. **A.** Fruit dominated browsers plotted against morphospace envelopes of browsers and grazers. **B.** Tapirs, suids, and elephantoids plotted against morphospace envelopes of browsers and grazers.

ilar to the phytoliths of grasses. *Tragulus* and *Moschus* feed on fruit as well, and they also fall close to the grazing domain probably for the same reason.

The two tapirs differ in their microwear. *Tapirus terrestris* falls within column 2 of table 2 and is close to some browsers and some mixed feeders; *Tapirus bairdii* falls within column 4 and is close to the grazing average scratch and pit morphospace shown in figure 11B. While, it is possible that *T. bairdii* feeds to some extent on forest grasses (Terwilliger, 1978; Padilla and Dowler, 1994), the high scratch results and results on the qualitative variables discussed below for both tapirs are most likely congruent with a dietary strategy involving the consumption of fair quantities of fruits and seeds. Both tapirs occupy the browsing-grazing transitional zone. This finding is new and significant for our understanding of the diet of tapirs.

Based on their average numbers of scratches, the suids fall between browsers and grazers (fig. 11B). Considering that suids often root (i.e., feed by digging into soils), the number of scratches is not as high as might be expected; that is, more scratches might be expected due to grit scoring the enamel surface. Our findings, although preliminary, do not support the hypothesis that grit and dust may cause an increased number of scratches on tooth enamel. However, some of the additional variables scored (described below) might be better indicators of the effect that grit might have on enamel surfaces. These additional microwear features support the fact that *Potamochoerus porcus* roots more than does *Hylochoerus meinertzhageni*.

The two elephants, *Loxodonta* and *Elephas*, fall within the browsing-grazing transitional phase (table 2). *Elephas* is closer to the grazers than is *Loxodonta*, and it has more scratches on average than does the latter (fig. 11B).

DISCRIMINANT ANALYSIS

A discriminant analysis was useful for classifying species into dietary groups and for gauging the degree of accuracy obtained in this classification process. The results of a discriminant analysis on extant taxa using only average pits versus average scratches as criterion variables and dietary categorization as a grouping variable demonstrate how clearly resolved browsing taxa are from grazing taxa. Figure 12 represents a graphical representation of the discriminant scores based on this analysis. Browsers cluster on the right side of the graph and are represented by circles. Grazers cluster on the left side of the graph and are represented by squares. There is no overlap between browsers and grazers. Mixed feeders have an interesting distribution and are represented by plus signs. They overlap both browsing and grazing realms depending on the relative amount of browse versus grass consumed (which would skew the average numbers of scratches up or down accordingly). Some mixed feeders occupy the gap between browsers

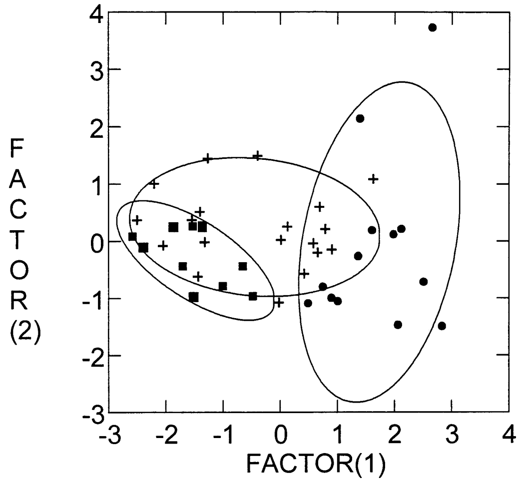

Fig. 12. Bivariate plot of discriminant analysis on extant ungulates using variables of average number of pits and scratches to discriminate between extant browsers (circles), grazers (squares), and mixed feeders (pluses).

and grazers because they consume fairly equivalent amounts of browse versus grass.

Table 3 represents the jackknifed classification matrix obtained from this discriminant analysis on living ungulates of known diets. Jackknifed results provide a meaningful evaluation of the discriminant function because the classification rule is not evaluated using the same cases employed to compute it, thus minimizing an overly optimistic estimate of the rule's success. Importantly, none of the extant browsers were misclassified as grazers and none of the extant grazers were misclassified as browsers. Twelve out of 12 extant browsers were correctly classified as browsers, giving an overall accuracy of discrimination of 100%. Seven out of nine extant grazers were correctly classified as grazers, and two grazers were misclassified as mixed feeders, giving an overall accuracy of discrimination of 78%. The situation with mixed feeders is less clear but is understandable and fairly predictable given the intermediate nature of their feeding habits. Only 38% of the mixed feeders were accurately assigned to the mixed feeding category based on average pits versus average scratches alone. Misclassification of mixed feeders is expected as their diets are mixed. The results make further sense by considering in what direction mixed feeders are misclassified. The findings are explainable in the sense that a mixed feeder incorrectly classified as a grazer is one that consumes a relatively high percentage of grass versus browse; a mixed feeder misclassified as a browser is one that consumes a relatively high percentage of browse versus grass. In the graph of scores from this discriminant analysis (fig. 12), such taxa are situated within the grazing or browsing clusters, respectively. Mixed feeding taxa in figure 12 which plot between the browsing and grazing domains are represented in the classification matrix (table 3) as the 6 out of a total of 16 mixed feeders correctly classified in the mixed feeding category (presumably eating a similar percentage of browse and grass). Thus, such taxa have average scratch numbers that fall intermediate to those of browsers and grazers and are discriminated accordingly. Fortunately, most mixed feeders are more easily discriminated from the other two dietary groups by examining a plot of absolute scratches found in individuals within a taxon and noting the characteristic bimodal distribution (see fig. 10).

TABLE 3

Probabilities from Discriminant Analysis
Jackknifed classification matrix. Variables = average number of scratches and pits

	B	G	MF	% Correct
B	12	0	0	100
G	0	7	2	78
MF	4	6	6	38
Total	16	13	8	68

B, browsers; G, grazers; MF, mixed feeders.

CLUSTER ANALYSES: EXTANT BROWSERS, GRAZERS, AND MIXED FEEDERS

Cluster analyses utilized both the average numbers of pits and scratches, percentages of raw scratches falling between 0 and 17, 17.5 and 29.5, and greater than 30, and the new microwear variables introduced in this study (see Methods).

BROWSERS: A hierarchical cluster analysis of extant browsers yielded a dichotomous splitting of species into two major clusters based on scratch textures (fig. 13). One-third of browsing species fall within a cluster of taxa grouped together based primarily on the

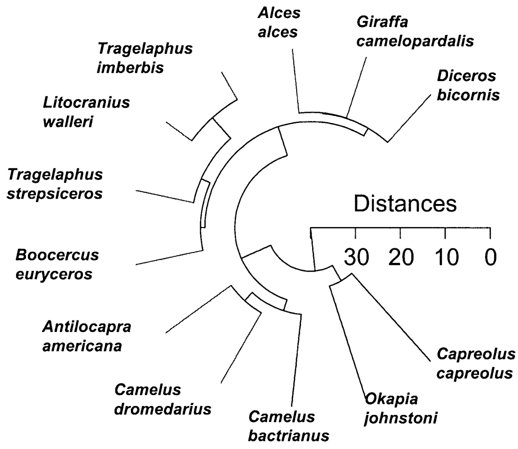

Fig. 13. Cluster tree of the extant browsers.

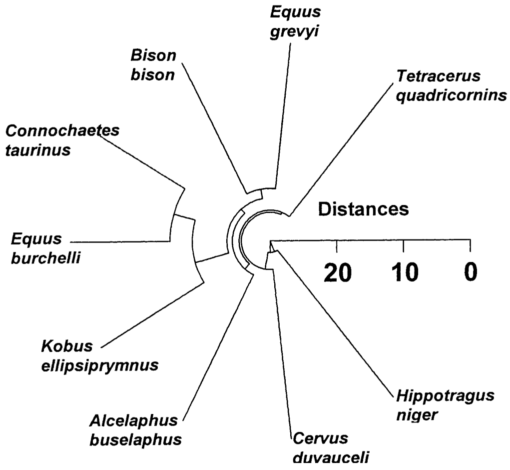

Fig. 14. Cluster tree of the extant grazers.

relative coarseness of scratches compared to the vast majority of browsers (cluster A below). Two-thirds of browsers cluster together mainly because the majority of their scratches are finely textured (cluster B).

CLUSTER A: COARSE-SCRATCH CLUSTER (*Antilocapra americana*, *Camelus bactrianus*, *Camelus dromedarius*, *Okapia johnstoni*, *Capreolus capreolus*): Unlike other browsing taxa, these taxa exhibit far fewer finely textured scratches and, conversely, more coarse or mixed-textured scratches than do other browsers. *Capreolus* and *Camelus* also have the highest number of pits of any of the extant browsers studied. *Capreolus* is also unusual because of the high numbers of scratches found within its enamel (within the middle of the grazing range). *Capreolus capreolus*, *Antilocapra Americana*, and *Okapia johnstoni* are also noteworthy due to the large percentage of large pits in their enamel as well as because of the relatively larger amount of coarsely textured scratches present than is typically seen in browsers. *Antilocapra americana* also has heavily gouged enamel, also atypical for most browsers.

CLUSTER B: FINE SCRATCH CLUSTER (*Alces alces*, *Boocercus euryceros*, *Diceros bicornis*, *Giraffa camelopardalis*, *Litocranius walleri*, *Tragelaphus imberbis*, *Tragelaphus strepsiceros*): This cluster of browsers has in common the fact that the vast majority of individuals within each species have finely textured scratches. Relative numbers of large pits, gouges, and cross scratches vary; specific details of individual taxa may be compared in table 1. Two subclusters are discernible—subcluster 1: coarse wear subcluster (*Boocercus euryceros*, *Litocranius walleri*, *Tragelaphus imberbis*, *Tragelaphus strepsiceros*), being taxa that display a fair number of individuals with large pits and relatively gouged enamel; and subcluster 2: fine wear subcluster: (*Alces alces*, *Diceros bicornis*, *Giraffa camelopardalis*), being taxa that cluster close together because they have the lowest number of individuals with large pits and no gouging of enamel.

GRAZERS: Extant grazers separate into four clusters based on their scratches (fig. 14). The majority of grazers have most scratches falling within the moderate scratch range (i.e., within the typical grazing average scratch morphospace shown in fig. 8). These taxa comprise cluster A shown below. A second cluster of grazers is distinguished by having relatively high scratch numbers (higher than the typical grazing scratch morphospace). These taxa comprise cluster B shown below. Two species separate themselves from these two main clusters due to the quality of their scratches rather than to their scratch quantities. Cluster C is defined by an absence of cross scratches. The single species occupying cluster C has scratches which run parallel to each other. This arrangement of scratches is unique among grazers, browsers, and mixed feeders with the exception of *C. natalensis* (a fruit/seed browser). Cluster D is defined by the high percentage of individuals within a taxon with finely textured scratches. One of the defining features of grazers based on this study is the relative paucity of fine scratch textures. Thus, this feature is unique among grazers.

Cluster A: Moderate-Scratch Cluster (*Equus grevyi, Bison bison, Connochaetes taurinus, Equus burchelli, Kobus ellipsiprymnus*): This cluster groups grazers with moderate numbers of scratches. The majority of grazers fall into this range of scratches. Other microwear features vary among the species grouped within this cluster (see table 1). Species with similar scar features are grouped closest together in the hierarchical cluster diagram.

Equus grevyi and *Bison bison* form a subgroup within this cluster. They are grouped together because they are the only grazers with significantly more purely coarse-textured scratches in individual enamel than with fine or mixed varieties. *Connochaetes taurinus* and *Equus burchelli* form a subcluster because they have relatively more scratches falling within the low scratch range (i.e. 0–17). Also, they have similar scratch texture patterns, that is, they have relatively more finely textured scratches than do other grazers (excluding *H. niger*). Concordantly, they have fewer purely coarse scratches as well, and most scratches are mixed (fine and coarse on the same tooth surface). These two species are very similar in the majority of their microwear features, although *E. burchelli* has a much more gouged enamel. *Kobus ellipsiprymnus* is similar to C. *taurinus* and *E. burchelli* in having the majority of its scratches falling in the moderate scratch range, although it has more small and large pits and fewer purely fine or purely coarse-textured scratches in its enamel. It groups close to cluster B taxa for two reasons: a relatively high percentage of its scratches fall within the high scratch range (30 or greater), and a high percentage of these scratches are of the mixed-textured variety.

Cluster B: High Scratch Cluster (*Cervus duvauceli, Alcelaphus buselaphus*): This cluster groups two grazers with a relatively high number of scratches that fall into the high scratch number range (30 or greater). A very high percentage of scratches are of the mixed scratch variety.

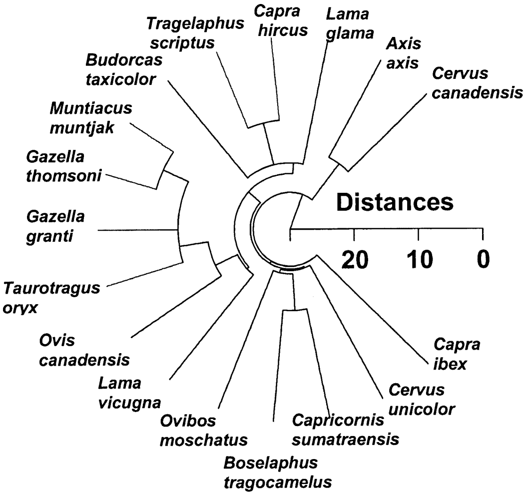

Fig. 15. Cluster tree of the extant mixed feeders.

Cluster C: Parallel Scratch Cluster (*Hippotragus niger*): *H. niger* is distinct from other grazers mainly because no cross scratches are present (i.e., scratches are almost always parallel to each other). It is also unique because no individuals have low or high scratch range scratch numbers. Consequently, all scratches fall within the medium scratch range (17.5–29.5).

Cluster D: Fine-Scratch Cluster (*Tetracerus quadricornis*): *T. quadricornis* is unique among the extant grazing taxa studied in having a very high percentage of finely textured scratches (as do extant browsers). It also has the highest percentage of individuals with large pits and gouging of its enamel as well as browsing-range small pit numbers.

Mixed Feeders: Mixed feeders sort into two major clusters based on relative scratch numbers (fig. 15).

Cluster A: High Scratch Cluster (*Axis axis, Cervus canadensis, Boselaphus tragocamelus, Capra ibex, Capricornis sumatraensis, Cervus unicolor, Ovibos moschatus*): Taxa in this cluster have average scratch numbers at the grazing end of the scratch range.

Cluster B: Low Scratch Cluster (*Lama glama, Capra hircus, Tragelaphus scriptus, Lama vicugna, Ovis canadensis, Taurotragus* *oryx, Gazella granti, Gazella thomsoni, Muntiacus muntjak*): These taxa have relatively low average scratch numbers. *Lama glama, Gazella thomsoni, Ovis canadensis,* and *Muntiacus muntjak* have average scratch numbers which fall within the gap between browsers and grazers in figure 9. *Capra hircus, Taurotragus oryx, Lama vicugna, Tragelaphus scriptus,* and *Gazella granti* have average scratch numbers that fall within the browsing range. Percentages of large pits and gouges are variable, as is the array of scratch textures. However, two subclusters can be distinguished—subcluster 1: coarse wear subcluster (*Gazella granti, Gazella thomsoni, Lama vicugna, Muntiacus muntjak, Ovis canadensis, Taurotragus oryx*): being taxa that may be distinguished by the relatively high numbers of individuals per taxon with gouging and large pitting of enamel (few finely textured scratches are present); and subcluster 2: fine wear subcluster (*Capra hircus, Lama glama, Tragelaphus scriptus*), being taxa that are distinguished by possessing the lowest degree of gouging, smallest numbers of large pits, and greatest percentages of finely textured scratches of the mixed feeders in cluster B.

New Dietary Categories

Results presented heretofore have discriminated between the broad dietary categories of browsers, grazers, and mixed feeders. The discrimination of taxa into these broad dietary categories was based on pit and scratch numbers. The following additional dietary categories may be distinguished, however, by adding the following variables to the analyses: large pits, gouges, and scratch textures.

Fruit/Seed Browsers: Figure 16 represents the results of a cluster analysis run using taxa with results typical of heavy fruit and seed browsing. These taxa display higher numbers of scratches than found in browsers (usually), higher percentages of coarsely or mixed types of scratches than found in traditional browsers or grazers, and very high percentages of large pits (table 2). In addition, the large pits seen in these taxa are very characteristic and unique. That is, they are the deepest pits that we observed (puncture-like) and are very symmetrical. We interpret these puncture pits to be due to the crushing of seeds consumed along with fruit. *Cephalophus* spp., *Moschus moschiferus, Tragulus* spp., *Muntiacus muntjak, Okapia johnstoni,* and *Tapirus* spp. are included in this category. However, there are individual differences which may have to do with the nature of the browse consumed, that is, with the relative hardness of fruit coverings and/or seed coats or with the relative amounts of these items consumed. These differences result in variable numbers of scratches, which are reflected in the spread from column 1 to 4 of table 2 and in the numbers of pits (fig. 11). Three of the four duikers have scratch numbers well outside typical browsing scratch ranges. *Cephalophus natalensis* has the highest number of scratches (within a grazing ungulate range). It differs however from grazers in the number and kind of pits. *Cephalophus dorsalis* and *C. silvicultor* also have high scratch numbers. Both taxa exhibit scratch numbers that fall within the gap between browsers and grazers and just outside of the lower boundary which defines grazing ungulates. *Cephalophus niger* stands out in terms of having scratch numbers within the typical browsing scratch range. This low-scratch result can most likely be explained by apparent differences in fruit and seed coat composition. *Cephalophus niger* apparently consumed fruits and seeds with relatively soft coverings compared to the other duikers studied. All of the duikers studied have numerous large pits (more than found in typical

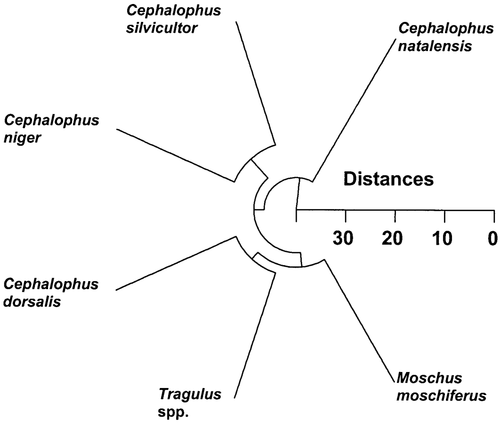

Fig. 16. Cluster tree of the extant fruit dominated browsers.

browsers or grazers). Gouging of the enamel in duikers is variable. *Cephalophus dorsalis* has the highest percentage of gouged enamel and *C. niger* is moderately gouged. However, both of the latter two taxa have enamel that is more gouged than in typical browsers; *C. silvicultor* is slightly gouged and *C. natalensis* has virtually no gouging of its enamel surfaces.

Two of the four duikers (*C. natalensis* and *C. silvicultor*) have individuals with scratch numbers that fall into the high scratch range (30 or greater). *Cephalophus niger* is the exception, with most scratches falling in the low-scratch number range characteristic of typical browsing ungulates. Standard browsers show a high percentage (three-quarters on average) of individuals within a taxon with purely fine-textured scratches. None of the duikers studied have percentages of finely textured scratches typical of other browsers, with the latter having a much larger percentage as a rule (exceptions are *Antilocapra*, *Camelus*, and *Capreolus*).

In *Cephalophus dorsalis*, *C. natalensis*, and *C. silvicultor*, most scratches in individuals are of the mixed variety, and thus many coarse scratches are present. *Cephalophus dorsalis* shows a high percentage of individuals with purely coarse-textured scratches. The percentage of individuals with purely coarse-textured scratches greatly exceeds that seen in typical grazers. *Cephalophus natalensis* has coarse scratch amounts within the range of typical grazing ungulates. It is possible that *C. dorsalis* and *C. natalensis* consume coarser fruits than do the other duikers studied.

Members of the genus *Tragulus* (browsing Asian tragulids) were analyzed and results were interesting. The tragulids studied here have average scratch patterns within the typical grazing range of scratches. Scratches also are predominantly coarse and mixed (similar to duikers but unlike typical browsers). *Tragulus spp*. (*T. meminna, T. napu*, and *T. javanicus*) display very low (for typical browsers or grazers) percentages of finely textured scratches and are most similar to *Cephalophus dorsalis* regarding the high percentage of coarse and mixed scratch textures observed. All of the individual teeth studied showed large pits, again similar to most duikers. Enamel was not gouged as a rule.

Moschus moschiferus has results consistent with fruit-browsing and microwear features very similar to those of *Tragulus*. Grazing-type average scratch numbers are present. *Moschus* differs from the duikers and *Tragulus* in terms of its relatively high percentage of scratches that fall in the high-scratch number range (30 or greater). *Moschus* also has high numbers of individuals with large pits. The enamel surface is not heavily gouged.

Okapia johnstoni is also placed in the category of fruit browsers, as the specimens have deep puncture pits and more and coarser scratches than typical leaf browsers. The same is true for *Muntiacus muntjak*.

BARK, COARSE STEM, AND LEAF FEEDERS: *Elephas maximus* and *Loxodonta africana* form this category which is defined by high scratch numbers and by very high percentages of purely coarse scratches, large pits, cross scratches, and gouges within the enamel surface. Scratches are hypercoarse and thus are coarser than those seen in any other extant taxa studied here (i.e., much deeper and wider). Both elephants display average numbers of scratches within the typical grazing range. Relatively few pits are present on average, but all individuals within both taxa display very high percentages of large pits, gouges, and cross scratches. In addition, very high percentages of purely coarse scratches are present. *Loxodonta africana* differs from *Elephas maximus* by having more pits, more gouges, and more cross scratches than does the latter.

ROOTERS: Two species of extant wild suids were studied, *Hylochoerus meinertzhageni* and *Potamochoerus porcus*. Both suid species show fairly similar scratch numbers and scratch distributions, although interesting differences regarding some of the additional new variables measured are observed. Both taxa have average numbers of scratches more typical of mixed feeders than of either browsers or grazers, which is understandable due to their omnivorous diets. Scratches are pretty evenly distributed between the low- and medium-scratch ranges, with none in the high-scratch range; both taxa have numerous cross scratches present. The interesting dif-

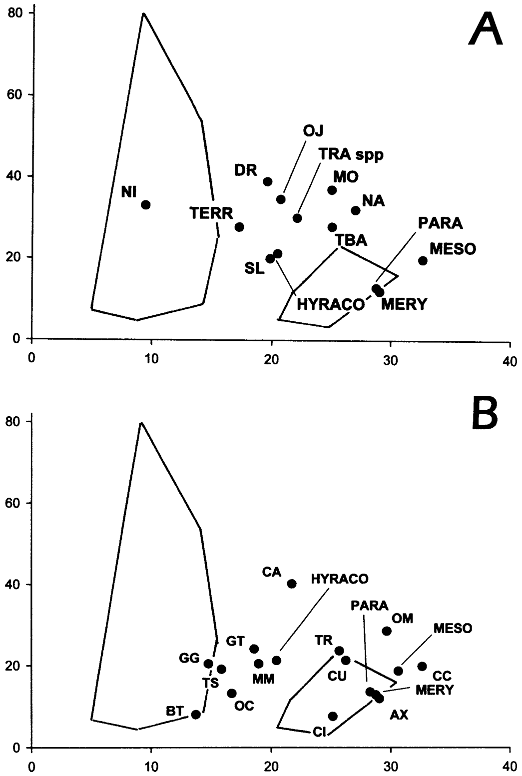

Fig. 17. Microwear in extinct equids showing marked dietary heterogeneity. **A.** Extinct equids plotted against fruit browsers. *Hyracotherium* falls near *Cephalopus silvicultor*. *Mesohippus, Parahippus,* and *Merychippus* differ from fruit browsers. **B.** Extinct equids plotted against selected mixed feeders. *Hyracotherium* falls near *Muntiacus muntjack*. *Mesohippus, Parahippus,* and *Merychippus* cluster together and are close to *Axis axis* and *Cervus canadensis*. There is a shift in the diet from *Mesohippus* to *Parahippus* and *Merychippus*. The latter two tend to graze more (shift by progressive reduction of pits and scratches). Morphospace envelopes of browsers and grazers are included in A and B.

ference between these two species involves the percentage of large pits, gouges, and coarsely textured scratches present. *Potamochoerus porcus* has very high numbers of individuals with large pits; *Hylochoerus meinertzhageni* has none. In addition, *H. meinertzhageni* has all finely textured scratches; *Potamochoerus porcus* has virtually none, but rather has a high percentage of coarse and mixed scratches.

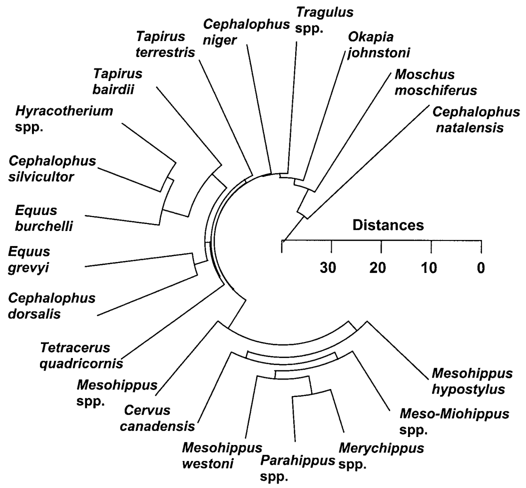

Fig. 18. Cluster tree of the extinct equids against selected species. *Hyracotherium* falls near *Cephalophus silvicultor*, a dietarily unusual large-sized duiker. *Mesohippus* falls near *Tapirus terrestris*. *Parahippus* and *Merychippus* fall near *Cervus canadensis*.

TAPIR BROWSERS: *Tapirus bairdii* and *T. terrestris* have different microwear patterns. *Tapirus bairdii* has grazing-range average scratch results, whereas *T. terrestris* has average scratch results on the high end of the browsing range. Scratch distribution patterns are also different. *Tapirus bairdii* is closer to many grazers and meal-by-meal mixed feeders than to browsers whereas *T. terrestris* is more similar to browsers and some seasonal or regional mixed feeders (see table 2). Tapirs have typically been regarded as browsing ungulates. However, relatively few individuals possess finely textured scratches typical of browsers. In addition, both tapirs have many individuals with large and deep puncturelike pits typical of fruit/seed browsers. Both tapirs have high numbers of individuals with cross scratches and no significant gouging in their dental enamel. *Tapirus bairdii* has results consistent with the consumption of coarser fruits and/or seeds than does *T. terrestris* (i.e., more and coarser scratches and more large pits).

FOSSIL EQUIDS: HYRACOTHERIUM

Hyracotherium (figs. 17 and 18) is distinguished from the other fossil horses studied by having the highest number of pits on average and an average scratch value which places it in the gap between extant browsers and grazers and closest to three fruit browsers regarding these two variables (*Cephalophus dorsalis*, *Cephalophus silvicultor*, *Cephalophus natalensis*, and *Tragulus* spp.). Considering, however, the distribution of scratches and the other variables, *Hyracotherium* spp. is most similar to *Cephalophus silvicultor*.

When fossil equids are included as unknowns in the discriminant analysis described in table 3, *Hyracotherium* is categorized with extant mixed feeders. This is because the discriminant analysis is based on only two variables (average number of pits and scratches) and fruit browsers were not included in the analysis. However, *Hyracotherium* plots away from the majority of mixed feeders when only these two variables are considered, with the latter concentrating closer to the browsing scratch/pit morphospace. When additional variables are included, a finer discrimination of diet ensues. Cluster analysis using all variables discussed in this study is more useful for determining dietary preference in terms of where the unknown extinct taxa might fall in relation to extant taxa of known diets (see fig. 18). When the additional variables are considered, *Hyracotherium* is most similar to the fruit browser *Cephalophus silvicultor*. In table 2, *Hyracotherium* and *C. silvicultor* fall in column 3 (within the browsing-grazing transitional zone).

When large pits, gouges, and scratch textures are considered, *Hyracotherium* displays a distinctly different pattern than do the other (and temporally later) equid taxa studied, with the latter taxa displaying very similar patterns to each other (although *M. westoni* is more similar to *Hyracotherium* in scratch numbers and scratch range distribution). *Hyracotherium* is distinguished by having many more large pits in its enamel; the other taxa have either no large pits or very few. These large pits are deep and puncturelike and have only been observed in this study in extant fruit browsers. All of the fossil equids studied have virtually no gouging of their enamel surfaces, but distinctly different scratch range distributions and textures are noted between *Hyracotherium* and the other fossil equids studied.

When raw scratch distributions are examined, *Hyracotherium* shows a bimodal scratch distribution typical of mixed feeders and fruit/seed browsers, with high-scratch and low-scratch subgroups. *Hyracotherium* distributes most of its scratches within the low-scratch percentage range; very few scratches fall within the high-scratch range. Scratches are equally distributed within the fine and mixed varieties. These scratch patterns are very different from the other fossil horse species studied.

FOSSIL EQUIDS: *MESOHIPPUS*, *MIOHIPPUS*, *PARAHIPPUS*, AND *MERYCHIPPUS*

Mesohippus spp., *Mesohippus bairdii*, *Mesohippus hypostylus*, a larger species than *M. bairdii* labeled as *Meso-Miohippus* in the AMNH collections, *Parahippus* spp., and *Merychippus insignis* group together in terms of microwear. These taxa have fewer pits on average than does *Hyracotherium*, and they have average scratch numbers within the standard grazing realm (e.g., *Mesohippus westoni*, *Meso-Miohippus*, *Parahippus* spp., and *Merychippus insignis*) or even higher than those seen in the extant grazers studied here (e.g., *Mesohippus* spp. and *Mesohippus hypostylus*). These latter high-scratch results are interesting because none of the modern grazers studied have such high average scratch numbers, nor do any of the mixed feeders. We think that these results reflect dietary differences from extant species. *Mesohippus hypostylus* is unique in having supernumerary scratch numbers only. We have found no modern analog for this latter type of microwear. *Mesohippus* spp. and *M. bairdii*, *Meso-Miohippus*, *Parahippus* spp., and *Merychippus insignis* distribute most of their scratches in the medium-scratch range (17.5–29.5) and high-scratch range (30 and greater). *Merychippus insignis* has the fewest number of scratches within the high-scratch range, most closely approximating the pattern seen in modern grazers (figs.17 and 18).

Discriminant analysis using the average number of pits and the average number of scratches places these later fossil horse taxa within or close to the extant grazing morphospace because of their high average scratch numbers and relatively few pits.

When raw scratch distributions are considered, these later horse taxa have unimodal scratch distributions with a high-scratch clustering of individuals typical of extant grazers and meal-by-meal mixed feeders (with the exception of *M. westoni*). In table 2, *M. westoni* is placed in column 3 with taxa which display three scratch ranges (low, medium, and high); *Mesohippus* spp., *Meso-Miohippus* spp., *Merychippus insignis,* and *Parahippus* spp. are placed in column 4 because they display two scratch ranges (medium and high). These results, in combination with the fact that these species have almost entirely fine scratches show that they are very different than traditional grazers (fig. 18). Examination of all the microwear data suggests that these species are most similar to *Cervus canadensis* (see Discussion). What is unique about this group of equids is the very high percentages of fine scratches found in individual teeth.

Interestingly, although *Mesohippus* and *Parahippus* are distinct from *Merychippus insignis* regarding gross dental anatomy, their microwear is only slightly different. The microwear of *Merychippus*, however, is closer to that seen in extant grazers (fewer pits, more scratches, similar scratch distributions) and hence in the expected evolutionary direction (Hayek et al., 1992).

MICROWEAR VERSUS OTHER DIETARY STUDIES

The results of this microwear study reveal a new dietary spectrum (table 2) that should be compared with other dietary studies to see how closely they match. We compare the results of this new spectrum with six studies.

(1) Schaller (1967: tables 10 and 11) provided specific dietary information (actual plants eaten) for several deer species inhabiting what is known as the Kanha Park. However, Schaller did not label the Kanha deer as browsers, mixed feeders, or grazers as such. Our microwear sample of these deer species is comprised mainly of teeth collected by Schaller at Kanha and donated to the Natural History Museum of London. Thus, we actually have samples from the same region and years as in Schaller's study.

By examining tables 10 and 11 from Schaller (1967), it appears that *Axis axis* is a mixed feeder. *Cervus unicolor* feeds on fewer species of trees and less grasses than does *Axis axis,* but overall, like *Axis,* it feeds on both browse and grass and it appears to be a mixed feeder as well. *Cervus duvauceli* feeds less on trees, but proportionally more on grasses, than do *Axis axis* and *Cervus unicolor*. Thus, Schaller's data and ours agree as to the basic diet of these three deer species.

(2) Bell (1971) established a grazing succession from the Serengeti involving plains zebra, topi, wildebeest, and sometimes the hartebeest and Thomson's gazelle (*Equus burchelli*, *Damaliscus korrigum*, *Connochaetes taurinus*, *Damaliscus hunteri*, and *Gazella thomsoni*). Bell observed that the zebra feeds first and is followed by the other species in a specific sequence. The zebra feeds on the rough higher grasses as it migrates. The removal of these grasses by the zebra enables the topi, the wildebeest, and the hartebeest to follow and feed on lower grasses left behind. Finally, the gazelle follows last, feeding on the smallest and softest vegetation that is accessible only after the removal of the taller grasses. The precise sequence of this succession is essential for these species to find their preferred vegetation. Mesowear data confirmed this succession (Fortelius and Solounias, 2000). The present microwear data confirms this succession as well such that the zebra and the gazelle bracket the other three species when scratch range distributions are considered (table 2).

(3) Hofmann and Stewart (1972) provided a subdivision of feeding in certain ruminants based on field observations and rumen structure. We find excellent agreement of microwear results and these field and rumen studies except for two species. *Tragelaphus strepsiceros* should be in column 1 of table 2, and *Tragelaphus scriptus* should not be with *Taurotragus oryx* and *Gazella thomsoni*.

(4) Jarman (1974) also provided various classes of ecology and feeding. We find Jarman's classes very difficult to relate to actual feeding as presented by Hofmann and Stew-

art (1972), and consequently we find little correspondence to those classes, especially with the duikers and the grazers where we see more detailed differentiation.

(5) Janis (1988) suggested a variety of trophic types on the basis of field data and hypsodonty. The regional/seasonal mixed feeders are similar in the two studies. Also, we find a matching pattern with Janis' categories of dry grass grazer and fresh grass grazer. Dry grass apparently etches coarser scratches into enamel than fresh grass, as fresh grass grazers such as *Connochaetes taurinus* and *Equus burchelli* have fewer coarsely textured scratches than coarse grass grazers such as *Bison bison* and *Equus grevyi*. However, we cannot, through microwear, distinguish high-level from regular browsing.

(6) Fortelius and Solounias (2000) established the method of dietary analysis known as mesowear, a method for dietary determination based on relative facet development. Mesowear is based on the physical properties of ungulate foods as reflected in the relative amounts of attritive and abrasive wear that they cause on the dental enamel of the occlusal surfaces. There are many common species examined by the mesowear method and the present microwear method. Actually, all common species are assigned the same type of broad dietary position with the exception of *Axis axis*, which is now placed in the mixed feeder category instead of the grazing category. The radical classification of ungulates provided in Fortelius and Solounias (2000) is the one established based on the present microwear data. Thus, the two studies are interrelated, although the sample numbers for each species are smaller in the present microwear study. In general, as expected, there is a good agreement between the two studies although a more detailed comprehensive comparison is in progress.

DISCUSSION

MICROWEAR RESEARCH

Microwear has been used to better understand the dietary habits of ungulates, primates, and other animals (Teaford and Walker, 1984; Teaford, 1985; Ungar and Kay 1995; Van Valkenburg et al., 1990; Hayek et al., 1992). Despite the well-established foundation for this technique, microwear has been underutilized compared to other modes of dietary analysis, mainly for logistical reasons. Two basic approaches have been used in microwear research. One approach has focused on understanding how food materials interact with tooth surfaces to cause microwear scar features (Ungar et al., 1995). Solounias' microwear work, as another approach, has focused on establishing diagnostic correlations between certain scar parameters and dietary behavior. This latter approach involves comparing an unknown pattern of wear (fossil ungulates) with a pattern where the diet is known (extant ungulates).

Plant foods show great variety in their material properties (e.g., relative hardness and abrasiveness). In addition to interspecies textural variations, different parts of the same plant may show variation. To complicate matters further, there is variation in hardness and abrasiveness according to the relative age of a plant. Furthermore, the relationship between microwear and the material properties of plants is not well known at this time. Another complicating factor involves the relative amount of food eaten by different animals, which would provide an additional source of variation. For example, wear due to a small branch which is eaten only 5% of the time by an animal may cause more wear on teeth than other, more abundant and commonly consumed foods. Another complication involves encountering museum specimens with little or, more commonly, no supportive collection data available. Correlating the diet of a particular species to its reported diet from a small field study in the wild, and then relating this to microwear data collected from different individuals, has limitations. These limitations become more apparent when one considers that many taxa feed on hundreds of plant species and display great variability regarding what they will feed on. Thus, there are many unavoidable difficulties involved in explaining precisely how vegetation produces wear patterns on teeth. Because of all these complications, we have concentrated on the diagnostic approach because much work needs to be done to adequately understand the interaction of food particles with tooth surfaces.

CORRELATION OF MICROWEAR RESULTS WITH AVAILABLE DIETARY INFORMATION

Diets of ungulates have been studied in the wild either by observation of animal behavior or by the analysis of fecal matter or actual stomach structure and/or stomach contents. Our microwear results agree well with published field data and they correlate with the broad dietary assignations given to extant species via these methods, although dietary assignations for certain species may need to be reexamined due to findings presented in the present study.

The new method is a viable technique for exploring the diets of ungulates, especially given the good correlation achieved between microwear results and previous dietary assignments (e.g., especially with Schaller's and Hofmann's results). In addition, the great simplicity and rapidity of our technique allow large sample sizes to be obtained. The value of the increased sample sizes as a result of this new technique should not be underestimated. For example, in more traditional studies it is important to consider how many animals might have been used to study rumen contents or how many fecal samples of a particular species might have been examined. Also, it is important to ask how representative such samples might be in determining the diet of a species, especially when considering the time depth of a species and the geographic variation of vegetation. Traditionally, such specimen numbers have been relatively low. Similarly, due to logistical constraints, how many wild individuals, and from how many different areas and time periods, do direct dietary observation studies include? With our new methodology, the number of specimens may be higher than in many other studies, except possibly for certain common species (e.g., *Gazella granti* or *Connochaetes taurinus*) that have been observed frequently in the wild. However, for rarer species where field data are poor, our microwear data may be a critical asset for future dietary understanding of extant species. In addition, a greater geographic breadth and temporal depth may be obtained, providing a specimen array from a richer and more abundant variety of locations spanning many more years of collection (roughly from 1900 to the present).

Although there is excellent agreement between the microwear results obtained here and the broad dietary information available from other sources, more precise comparisons are difficult. Most field methods are single-species studies (e.g., studies on various deer). Consequently, these studies report dietary data and patterns that cannot be easily summarized under a unified standard, as they differ in details and methodologies. The specificity of such results cannot yet be directly compared to those obtained via microwear at the present time. For example, a species feeding 20% of the time on twigs and 80% of the time on wet grasses cannot be clearly related to a specific categorization beyond that of mixed feeder or grazer, which is the level used in our study. Moreover, there are only a few studies available where groups of species have been studied by the same researcher. Such studies have been the most useful to us (e.g., Schaller, 1967; Hofmann and Steward, 1972; Hofmann, 1973; Jarman, 1974; Hofmann, 1985).

NEW INTERPRETATIONS ABOUT UNGULATE DIETS

Tooth microwear analysis at low magnification with a light microscope not only successfully classifies many Recent ungulate species into conventional dietary categories, but it also offers additional resolution within these categories (see cluster analyses; table 2). Although previous microwear research recognized only two scratch ranges at 500× (0–27 for browsers; 40–60 for grazers; Solounias et al., 2000a), we now recognize three ranges which amplify themselves into five biologically meaningful combinations. It is highly probable that these scratch range patterns have a natural basis because they are based on patterns of scratch counts of many individuals per species. We also observe that substantial pitting and gouging and coarseness in scratch texture in certain species (e.g., camels, llama, pronghorn, and suids) may be related to grit in the diet. These distinctions have not been discerned by other methodologies (e.g., previous microwear studies, snout analyses, hypsodonty indices, or masseteric analyses). Such distinctions, as well as what we call here the browsing-grazing transitional zone, make sense in terms of evolutionary transitions and should be explored further in conjunction with mesowear, hypsodonty, and tooth structure.

The five-part subdivision of diets is a new and promising finding, as it offers greater resolution within the standard trophic categories of browsing, grazing, and mixed feeding. By sorting species in this way, a progressive reduction in the number of browsers is encountered as one moves from the left to right side of table 2. The number of grazing species increases as one moves in the opposite direction in table 2, although the reduction in the number of browsers is more abrupt (i.e., most browsers are restricted to columns 1 and 2). The grazers, however, show a more heterogeneous spread throughout the columns. From an evolutionary standpoint, it might follow that some type of grazing may enhance expansion into new habitats as long as a variety of habitats exists. Similarly, browsing may be more restrictive in terms of allowing for such an expansion.

Mixed feeders can be identified as two types: seasonal or regional mixed feeders and meal-by-meal mixed feeders. Seasonal mixed feeders vary their diets according to rainfall and seasonal variations in vegetation. When they migrate they may alter their diet according to the availability of browse or grass. Hofmann (1973) described only seasonal or regional mixed feeders. Mixed feeding ungulates are unevenly distributed according to their scratch distributions. Seasonal or regional mixed feeders are concentrated closer to browsers and to species that display high attrition (table 2: columns 2 and 3). When these species browse, they have microwear results similar to those of traditional browsers. However, when these same taxa graze, their results differ from those of grazers by having more pits than are seen in the latter species. Our results indicate that such mixed feeders typically display a greater dispersion of scratch numbers than is typically seen in extant grazers (fig. 8C versus 8A and 8B). Such differences between mixed feeders that graze and true grazers are interesting. It is possible that pits obtained during the browsing phase of these animals remain on tooth surfaces as additional scratches obtained during a grazing phase are made. Such patterns might be useful in terms of examining seasonality in extinct taxa.

Meal-by-meal mixed feeders vary their diets on a daily basis rather than on a seasonal or regional basis. No discernible browsing versus grazing subgroups are apparent. The meal-by-meal mixed feeders are all concentrated closer to the grazers and to species that display high abrasion (table 2) according to their scratch distributions. This pattern has never been noted in prior studies. Although grazers evolved from browsers independently on numerous occasions, it is possible that in the origin of grazing from browsing, the first step might have involved regional or seasonal mixed feeding. Such mixed feeders might have shifted to a meal-by-meal pattern as species moved closer to adopting a grazing strategy. Interestingly, this type of mixed feeding does not appear to be prevalent in Africa based on the database presented here. Consequently, Hofmann (1972) did not note the meal-by-meal mixed feeding adaptation in ungulates since his work was based on East African ungulates. Although our data are far from complete, it is possible that grazing may have evolved in Asia from mixed feeders ecomorphically similar to those found in column 4 of table 2. This finding should be kept in mind in the future when interpreting the diet of extinct species and the evolution of ungulate communities.

One difference in the present study from most previous microwear studies is the finding that certain nongrazing extant taxa have individuals with apparent scratch counts higher than those seen in typical modern grazers (the latter species are shown in column 5 of table 2). This pattern was also observed at 500× magnification (Solounias et al., 2000a). We think that taxa displaying these high scratch counts may possess fewer scratches than do typical grazers (despite the scratch numbers) due to an underestimation of the actual scratches present in the latter. This conclusion is based on differences in the appearance of the enamel surfaces of teeth with many scratches versus teeth with few scratches. Note that this is not an artifact of lower magnification or resolution, as this same phenomenon was observed using SEM at 500× magnification.

To adequately explain this phenomenon, the difference in appearance of scratches against a scratch-free versus a heavily scratched enamel surface background must be considered. The tooth surfaces of ungulates of all trophic categories are affected by the forces of attrition and abrasion acting simultaneously (logical expectation). Attrition results in planar wear from tooth-to-tooth contact after relatively soft foods have been completely cut by teeth. Abrasion produces rougher surface wear imposed by food-to-tooth contact by more abrasive food items. Both attrition and abrasion are thought to occur at all times during mastication, and the resulting tooth wear can be attributed to both processes (Fortelius and Solounias, 2000). In browsers, abrasion is relatively low and attrition relatively high. The result is a relatively flat and shiny (polished) enamel surface where scratches are clearly seen and are separated from each other by areas of nonscratched enamel. Thus, the scratches of browsers appear very distinct against an unscratched and smooth enamel background. In grazers, where abrasion is high and attrition is relatively low, attrition effects are masked; as a result, the background enamel surface is duller and more etched and uneven. The high abrasion imposed by significant grass (phytoliths) in the diet of these animals also significantly etches the enamel surfaces. Scratches fall upon other scratches, often with little or no nonscratched enamel surface between them.

Consequently, we think that we are undercounting the true number of scratches for certain grazers. The apparently high scratch counts that we have observed in some nongrazing specimens are most likely a reflection of the difficulty of resolving separate scratches in grazers rather than due to a higher absolute number of scratches present in nongrazers. An analogy for understanding this idea involves envisioning an ice-skating rink, the surface of which represents the enamel surface. Individual skate cutmarks (analogous to scratches induced by phytoliths) are difficult to distinguish on an overused rink surface, but are they are highly apparent when the ice has been newly smoothed and underused.

Dietary microwear patterns obtained sometimes conflict with field results. The finding of such contradictions is interesting and valuable and should eventually be critically reexamined by additional field observations and/or microwear studies. For example, we have observed that some animals classified as browsers have patterns that are distinctive from other browsers. Thus, the tapirs, duikers, okapi, *Capreolus capreolus*, *Tragulus*, and *Moschus* taxa studied show scratches that are atypical for traditional browsers (i.e., scratches are coarsely textured) and they often display relatively high scratch numbers and an exceedingly large number of large, deep pits. These patterns are most likely due to fruit and seed feeding. Fortelius and Solounias (2000) have also found duikers to be distinct from other browsers in their mesowear patterns. *Cervus canadensis*, *Cervus unicolor*, *Ovibos moschatus*, and *Capra ibex*, previously thought of as seasonal or regional mixed feeders or as grazers, are placed in our newly discovered category of meal-by-meal mixed feeding.

Two types of scratches are distinguished: coarse and fine. Coarse scratches are typical of C4 grazers, bark eaters, and fruit browsers and may be due to hard fruit and seed coverings, or coarse bark and stems. Fine scratches are typical of leaf-eating browsers and certain mixed feeders, such as *Capricornis sumatraensis*, *Cervus canadensis*, and *Budorcas taxicolor*. Consumption of C3 grasses would explain the observed pattern. The previously mentioned species inhabit forests or mountainous regions covered by forests where C3 grasses grow. Fine scratches are also typical of the mixed feeder *Lama glama*, which inhabits nonforested alpine grassland that is also composed of C3 grasses that grow at high altitudes.

Our data provide some resolution as to the effect that grit might have on dental enamel. Interesting patterns of microwear are seen in species that have in common the occupancy of dry, open habitats (camels, pronghorn antelope, and vicugna) or which root in substrate (African bush pig). All of these taxa have large percentages of either purely coarse or mixed coarse and fine scratches relative to others in their respective trophic groups. Increased pit numbers (small and/or large) are also present in these taxa as are moderate to large amounts of gouging of the enamel surface. These results indicate coarser wear than expected based on results found in other members of the trophic groups involved. Such results parallel to a certain degree what is seen in grazing ungulates. The groups can be distinguished, however, since grazers will have a homogeneous high average number of scratches whereas the other groups will have homogenous low or bimodal distributions. Grazing ungulates in general have a greater percentage of coarse scratches, gouges, and large pits than do nongrazing ungulates, with the former presumably encountering more grit simply because of the manner of feeding on grass versus browse (i.e., closer to the ground and often cutting vegetation close to the soil surface).

Camelus bactrianus and *Camelus dromedarius* are distinctive among other browsers by their very high average pit numbers. Both taxa also have very low percentages of individuals with fine scratches, which is not the typical pattern seen in browsing ungulates. Relatively high percentages of individuals are present with purely coarse and mixed type scratches. The bactrian camel also has more pits on average, more large pitting, and more gouging of its enamel than does the dromedary. Camels occupy arid desert and steppe habitats, and heavy pitting, gouging, and coarser scratches than is typical for browsers may be the result of grit.

The pronghorn is also distinctive among our browsers by having very low percentages of individuals with fine scratches. No purely coarse scratches are present in individuals, as is seen in the camels and vicugna. Most scratches are a mixture of coarse and fine textures. Based on lower average pit numbers and fewer coarse scratches, it is probable that the pronghorn consumes less grit than do the camels or vicugna. In addition, although several studies report that the pronghorn is a mixed feeder (see Byers, 1997: 29), we find that it is a browser, which is surprising given its hypsodonty. Our result is supported by a very large sample. Other researchers have also found low percentages of grasses in the pronghorn diet (Smoliak, 1971; Hansen and Clark, 1977; Olsen and Hansen, 1977).

The camelid *Llama vicugna* is unusual among mixed feeders by possessing very high percentages of purely coarsely textured scratches and heavily gouged enamel. Relatively high pit numbers are also present. The vicugna occupies arid grasslands and plains of the High Andes Mountains and we think that the coarse scratches, heavy pitting, and gouges are due to the occupation of an arid environment where grit encroaches upon food materials.

Many suids are primarily rooters, that is, they use their snouts as plows to root up vegetation that is beneath the soil while foraging for roots and other such food materials. Interestingly, *Potamochoerus porcus*, a committed rooter, has very different microwear from *Hylochoerus meinertzhageni*, which primarily forages and does not do much digging. Both suid species show fairly similar pit and scratch numbers (*P. porcus* has relatively more of both), but interesting differences exist regarding some of the additional new variables measured. Both species have average numbers of scratches more typical of mixed feeders than found in either browsers or grazers, which is understandable due to their omnivorous diets. The interesting difference between these two taxa has to do with the percentage of large pits, gouges, and coarsely textured scratches present. *Potamochoerus porcus* has very high numbers of individuals with large pits and gouges; *Hylochoerus meinertzhageni* has no individuals with large pits and no gouging whatsoever of its enamel surfaces. In addition, while all individuals of *H. meinertzhageni* have finely textured scratches, virtually no individuals of *P. porcus* have fine scratches, but rather, a high percentage of individuals with coarse and mixed scratches are seen. It is probable that the large pits, coarse scratches, and gouges in the enamel of *P. porcus* reflect its higher degree of rooting compared to *H. meinertzhageni*. Within suids, it may be possible to discern the relative degree of rooting behavior using these variables.

These results indicate that a high degree of pitting, coarse scratching, and gouging of dental enamel may provide insight regarding the occupation of open and arid habitats and rooting activities in ungulates.

Finally, the two Proboscidea (*Elephas maximus* and *Loxodonta africana*) are distinct from each other, which is surprising considering the coarseness of their foods. It is also surprising to see a low number of pits overall in the elephants. It would seem likely that the consumption of tree branches and bark would form a substantial number of pits. *Diceros bicornis* also feeds on small branches, however, and has a low number of pits and scratches. Thus, within the Proboscidea, large percentages of individuals possess large pits, although this is not the case for *D. bicornis*. Consequently, it is likely that the elephants consume either more bark or a tougher variety of bark than does *Diceros*. The latter subsists more on thin, regenerating twigs, whereas the former subsists on tough bark. It is clear that the question of how most pits are generated in browsers requires additional study.

NEW MICROWEAR VARIABLES

The new microwear features introduced in this study have proven to be interesting. By scoring large versus small pits, gouging, and different scratch textures, we have been able to define new subcategories within browsers, that is, fruit/seed eaters and bark eaters. In addition, within the suids, it has become possible to distinguish different degrees of rooting behavior and to identify taxa that most likely consume fairly substantial quantities of grit in the arid and open habitats that they occupy.

We are particularly intrigued by the differences in scratch textures encountered. Excessive numbers of fine scratches are seen in some high-altitude animals included in our database (e.g., *Capricornis sumatraensis*, *Budorcas taxicolor*, *Lama glama*) as well as in forest animals and most of the fossil equids. Also, browsing ungulates have mostly fine scratch textures, whereas open grassland grazers have more coarsely textured scratches. These findings suggest that fine scratches may be related to the consumption of C3 grasses (fine), whereas C4 grasses might impose coarser scratch textures. These findings are promising in light of new information which suggests that there may be differences in phytolith sizes. The direction of future research will be challenging since Solounias and Hayek (1993) found no significant differences in the widths of scratches at the 500× magnification.

By increasing the number of microwear variables, cluster analysis revealed interesting subgroups within the dietary categories of browser, grazer, and mixed feeder. Thus, a fine scratch versus a more coarse scratch polarization of browsers was obtained as were numerous subgroups distinguished by relative amounts of gouging, pitting, and scratch numbers present in various taxa. Typical grazers were defined by a relative paucity of pits, and a preponderance of either fine scratches (C3 grazers), coarse scratches (C4 coarse grass grazers), or a mixture of fine and coarse scratches (C4 fresh grass or mixed grass grazers). Mixed feeders were polarized into low-scratch versus high-scratch groups representing the relative amount of browse versus grass consumed in the diet, and taxa with more scratches than found in typical grazers were identified.

COMPARISON TO PREVIOUS MICROWEAR STUDIES

Overall, the results obtained with the light microscope are similar to those obtained in the past with much higher magnifications. In a practical sense, what is most important with studies of this nature is an accurate diagnosis of diet, rather than the ability to see more microwear features. Scratches have again proven to be more diagnostic than pits for determining the dietary categories of browsers, grazers, and mixed feeders (e.g., Solounias and Hayek, 1993). Undeniably, SEM is superior for attaining the type of resolution necessary for certain types of research and for obtaining clear photographs. However, the smaller magnification (larger visual field) involved in this new method gives the researcher more control in selecting a truly representative area on the tooth surface to obtain accurate counts (e.g., scars due to food materials rather than postmortem damage). In addition, SEM is expensive and it takes a long time to analyze specimens. Also, comparisons are usually limited to the available photomicrographs of a particular area of a specimen. Although it takes several days with SEM to analyze a species, provided there are no processing or equipment problems, a species can be analyzed in a couple of hours with the new method. Therefore, comparisons between specimens are very easy to make, as one can have several specimens next to the microscope that can be switched back and forth.

Unpublished comparative studies show that all of the features that are seen with the light microscope are part of the higher-magnification photomicrographs in prior studies. Interestingly, quantification of many parameters provided by the SEM methodology (e.g., mathematically estimated areas of pits, digitized lengths of pits and scratches) has provided little useful information. For example, Solounias and Hayek (1993) determined that the lengths of long scratches were not as significant as scratch numbers, as most scratches measured had artificially cropped lengths imposed by the rectangular shape of photomicrographs. Short scratches within the field were significant. The actual lengths of scratches that originated in the counting field and extended beyond it could not be measured. Many of the quantifications obtained via the high-tech SEM methodology were not useful in diagnosing dietary behavior.

Crown Height, Mesowear, and Microwear

Until now, the best established gross morphological predictor of diet in ungulates has been thought to be crown height (Janis, 1988), which represents a main aspect of functional tooth durability in terms of wear (Janis and Fortelius, 1988). In simple terms, crown height is the degree of height of enamel of a tooth in relation to its width, which is typically measured by various hypsodonty indices. For example, Janis (1988) measured the width of the third lower molar near, but not at, the occlusal surface and divided this width by its length (cement is excluded in these types of measurements; Janis, 1995 personal commun.).

However, crown height should perhaps be conceived of as a proxy for overall wear rate (Solounias et al., 1994), much as mesowear variables are best conceived of as proxies for certain kinds of wear. It is becoming increasingly clear to us that crown height is the result of numerous factors such as attrition, abrasion, and grit in food items and it represents the adaptation of a species in deep time. Fortelius and Solounias (2000) found that mesowear analysis provides resolution within the main dietary classes of ungulates and that clustering is virtually identical with and without the inclusion of an index of hypsodonty. They also found that mesowear variables produce clusters that appear biologically more distinct than do clusters based on hypsodonty alone. Because crown height is essentially a reflection of overall wear rate, its relationship to food properties should be expected to be considerably less specific than mesowear or microwear.

When hypsodont, mesodont, and brachydont species are examined against the microwear results summarized in table 2, no clear pattern emerges. Hypsodont species are found in all five columns. We speculate that the hypsodont species found in columns 1 and 2 are mostly hypsodont due to high attrition in their dietary behavior (*Capra hircus*, *Ovis canadensis*, *Budorcas taxicolor*, and *Boselaphus tragocamelus*) or possibly because of exposure to large amounts of grit (camels, llama, pronghorn). Hypsodont species found in columns 4 and 5 of table 2 are species with abrasion-dominated diets. The same patterns can be argued for the mesodont species. It is argued here that since hypsodonty can be the result of attrition, abrasion, and grit, it is not a sensitive indicator of diet per se.

One can develop a time sequence by using tooth morphology, including crown height, mesowear, and microwear. (1) We think that crown height and gross tooth morphology are adaptations that encompass the requirements for everyday feeding, but also reflect long-term evolutionary dietary habits (which may exceed the lifespan of an individual animal and the range of human investigations). Crown height and other gross tooth morphological features represent adaptations at the species level. (2) Mesowear is the additive and average end result of several years of feeding. Mesowear is useful in reflecting the overall wear of an individual over several years of feeding behavior (Fortelius and Solounias, 2000). It represents cumulative wear over the lifetime of an animal. (3) Microwear is the shortest lasting of the three domains, but it is the only one that directly relates to foods eaten. Microwear most likely is the result of a few days of feeding behavior. Solounias et al. (1994) have shown that rates of tooth wear are high enough that microwear will be wiped off the enamel surface and will change every few days; new microwear replaces the older microwear. Thus, hypsodonty, mesowear, and microwear offer glimpses into different time-slices in the evolutionary and ecological histories of taxa. Ultimately these three aspects of diet and morphology should be studied together.

THE NEW METHOD

Previous microwear studies have been limited to the use of the average number of scratches and pits for determining diet. We currently use additional information, namely the average number of scratches and pits in combination with the relative size of pits, relative numbers of individuals in a taxon with gouges, and certain types of scratches (fine, coarse, mixed), as well as raw scratch ranges to determine a match between extinct and extant forms.

The ability to process more specimens and species (without the SEM constraints) has proven essential for the accurate diagnosis of diet and for an adequate representation of diverse ungulate taxa. For example, several perissodactyls and additional artiodactyls as well as proboscideans are represented for the first time in the new database. Also, most previous ungulate studies have focused on the attractive and rich African faunas. A good representation of Asian and American species, as well more African species, is now available for comparative purposes. In fact, the present study has shown better resolution of specific dietary habits than that obtained in previous studies because of the insights gained from the Eurasian samples. Hopefully, these findings will be used to reexamine what is known about diets of ungulates and to resolve various questions regarding them. Some examples of interesting questions are as follows: What specifically causes pitting of enamel? How relevant is grit in determining microwear and crown height? What are the biological differences and ecological constraints found among the various mixed feeders? Does the dietary variation seen in browsers and grazers have other biological support? How are the new findings related to the size of masseteric muscles, differences between continents, and altitudes?

FOSSIL EQUIDS

The results on *Hyracotherium* are preliminary (a more detailed and specific study is underway). The microwear of *Hyracotherium* sensu lato showed that it is most similar to that of the duiker *Cephalophus silvicultor*. However, when only the average number of pits and scratches is considered, it is most similar to *Cephalophus dorsalis*. These two duikers have similar microwear, but there are some differences such as the average number of pits. When crown height, gross tooth anatomy, and deep puncturelike pits are considered, it is likely that *Hyracotherium* was a fruit/seed-eating browser and that the average scratch numbers which place it in the gap between browsers and grazers are due to a scratching of enamel by hard fruit and/or seed covers as in other fruit and seed browsers. For example, *Hyracotherium* is brachydont and shows gross toothwear patterns consistent with living species which consume fruit, nuts, or seeds in their dietary regimes as well as leaves (Janis, 1990).

Mesohippus spp. (and *M. bairdii*), *Mesohippus hypostylus*, *Meso-Miohippus*, *Parahippus* spp., and *Merychippus insignis* cluster very tightly together. They are characterized by numerous fine scratches and fine wear overall (virtually no gouges or large pits are present). Based only on their high scratch numbers and unimodal scratch distributions, the taxa studied could be either meal-by-meal mixed feeders or unique grazers with no modern analogs. When other variables are considered, such as scratch textures, large pits, and gouges, these later horses are unlike any modern grazers, despite their high average scratch numbers.

Of these later extinct equids, only *M. insignis* has been included in prior microwear studies (Hayek et al., 1992) and in the recent mesowear study (Fortelius and Solounias, 2000). Interestingly, different trophic assignments were given to this taxon based on these two methodologies. Microwear (using SEM at 500×) placed *M. insignis* with extant grazers, whereas mesowear analysis of this taxon clustered it with the abrasion-dominated mixed feeders. It is important to realize that any high-scratch taxon in prior microwear studies was assigned to the grazing category. By incorporating many more extant species into the comparative microwear database in this study, it is now evident that meal-by-meal mixed feeders are indistinguishable from grazers in terms of their unimodal scratch distributions and grazing range scratch numbers, and this trophic strategy must be considered when high scratch results are obtained.

Mesohippus, *Meso-Miohippus*, *Merychippus*, and *Parahippus* were either meal-by-meal mixed feeders or C3 grazers. Considering the present extant species of our database, there are little differences between these two categories. These extinct species plot near the grazers (high average of scratches) but their scratches differ in being very fine. One extant mixed feeder, the wapiti (*Cervus canadensis*), also has high percentages of finely textured scratches, and it falls into column 4 of table 2 with these fossils. It is likely that the finely textured scratches of *C. canadensis*, which inhabits forests, forest margins, and high elevation areas, might have to do with the consumption of C3 grasses. The same was probably true for the extinct species in question. Thus, *C. canadensis* can be considered as a good ecomorph for these particular extinct species. The only other modern grazer that has such a high percentage of fine scratches is the chousingha (*T. quadricornis*). The specimens of *T. quadricornis* used in this study are from India, where they are most frequently found in monsoonal forests. The habitat preference of *T. quadricornis*, coupled with its fine-scratch pattern, indicates that it is also most probably a C3 grazer. As such, it is another useful species and can also be used as an extant model of a C3 grazer for comparative purposes.

Mesohippus, *Meso-Miohippus*, *Merychippus*, and *Parahippus* are most similar to *C. canadensis* but they differ markedly from *Tetracerus quadricornis* in several of their microwear features. Despite sharing similarities in scratch textures, *T. quadricornis* has significantly more large pits and gouging of its enamel, as well as a different scratch distribution pattern (i.e., relatively few scratches are in the high scratch range) and fewer countable scratches on average, than do these fossil horses. These results are consistent with the consumption of more grass by *T. quadricornis* than by *C. canadensis*.

Mesohippus, *Meso-Miohippus*, *Merychippus*, and *Parahippus* are most similar to *C. canadensis* in scratch numbers, scratch distributions, scratch textures, and relative amounts of pitting and gouging. Their microwear is thus consistent with meal-by-meal mixed feeding. It is also most probable that these taxa were consuming a significant amount of C3 grasses during the grazing phase of a meal-by-meal mixed feeding pattern.

A finer dietary differentiation is observed within the evolutionary progression of *Mesohippus* to *Parahippus* to *Merychippus*. A progressive decrease in both the numbers of scratches and pits is discerned. For example, if the average number of pits is examined, species sort according to a decreasing number of pits as one moves along the general evolutionary sequence of fossil horses; that is, from *Hyracotherium* (21) to *Mesohippus* (16) to *Parahippus* (13) to *Merychippus* (12). The lowest numbers of pits are seen in the extant horses analyzed: *Equus burchelli* (11) and *Equus grevyi* (8).

A similar pattern is also seen when the numbers of scratches are followed through geologic time. However, we remind readers that over-scratched teeth (column 5 of table 2) show less countable scratches than those of columns 3 and 4 due to the superimposition of one scratch upon another (see Results and appropriate section of Discussion). Scratches slightly decrease from *Mesohippus* (30) to *Parahippus* (29) and *Merychippus* (29). The lowest numbers of scratches are seen in the extant horses: *Equus burchelli* (22) and *Equus grevyi* (26). *Merychippus insignis* approximates modern grazers more than the others, if the distribution of scratches is considered. In *Merychippus insignis*, most scratches fall in the medium scratch range (17.5–29.5). Thus, there is a decrease in the number of scratches in the fossil horses studied through time, with the exception of *Hyracotherium* (21), which most likely attained some of its scratches through hard fruit and seed covers, as in extant duikers. *Merychippus* (*Cormohipparion*) *goorisi* was also found to be grazing in a previous study (Hayek et al., 1992). Such a decrease in scratches reflects an increase in grass consumption.

Interestingly, in the transition from *Mesohippus to Parahippus* to *Merychippus*, there is a notable gross dental change. In *Mesohippus* and *Parahippus*, molars form simple distinct crests and are brachydont. In *Merychippus*, lophs become embedded in a thick layer of cementum, and each loph takes the form of tubular selene instead of a simple crest. In addition, the teeth are notably more hypsodont in *Merychippus*. Rensberger et al. (1984) found that there is a notable change in chewing as well with the *Merychippus* type of teeth. With regard to chewing, *Merychippus* is more similar to *Equus* than to *Mesohippus*. These changes in tooth morphology and function are major, but microwear differences are slight. Nevertheless, the dental transition is supported by a dietary change in the expected direction (toward more grass feeding), although evidence is presented here that the browsing to grazing transition in horse evolution most likely did not involve the encroachment of C4 grasslands. Instead, it is more likely that grazing in horses involved the consumption of C3 grasses in forests, most likely beginning via a meal-by-meal mixed feeding strategy. The extinct equids studied here appear to be occupying a different niche than modern grazers. All of these findings pave the way for additional research regarding the reasons for these differences (i.e., habitat and dietary differences).

CONCLUSIONS

A new simplified methodology at 35× magnification for the assessment of dietary adaptations of living and fossil taxa has been developed which diminishes the need for a scanning electron microscope for the study of tooth microwear. The simplicity and relative rapidity of this new methodology provide a mechanism for greatly increasing the number of specimens typically analyzed per species in microwear studies. In addition, a notable increase in the number and breadth of species included within a new and expansive extant microwear comparative database has become possible.

This new database is improved over prior SEM databases such that now several additional artiodactyls are represented (e.g., primitive ruminants, camelids, and suids), and perissodactyls (horses, tapirs, and rhinos) are represented for the first time. Also, the Eurasian ungulate fauna is now better represented in addition to a more expansive African fauna, thus providing more biogeographic as well as temporal depth to the database. These advancements in microwear logistics and sampling capabilities may help solve underutilization of this valuable aid in dietary reconstruction. In addition, several new insights into the evolution and application of ungulate trophic strategies have come out of this research because of the elucidation of patterns that could not have been discerned without large sample numbers. For example, although not the primary focus of this study, a better understanding of the interaction of various food materials and grit with dental enamel in producing certain microwear scars is evident for the first time. For instance, it is now possible to use the texture of scratches to discern possible C3 versus C4 grass eating; the preponderance of coarse scratches and large and deep puncturelike pits to discern fruit and seed browsing; the finding of numerous hypercoarse scratches, cross scratches and gouging to discern bark and coarse-stem feeding; and a heavily pitted, gouged, and coarsely scratched enamel surface to discern significant rooting behavior in suids. In addition, it appears that the incorporation of grit into the diet does not produce differences in the quantity of scratches, as expected, but rather it produces qualitative differences in scratch texture and pitting and gouging of enamel.

Many important paleoecological insights may be gleaned from this work as well. The grouping of modern taxa into three main trophic phases based on scratch distributions has led to a better understanding of ungulate niche separation and evolution. For example, it is now evident that browsers, grazers, and mixed feeders are more heterogeneous dietary groups than reported previously. Thus, browsers are separated into two main subgroups based on scratch textures, with the fine-scratch subgroup being further subdivided based upon the relative coarseness of other scar features (i.e., relative amounts of large pits and gouging of enamel). Grazers are separated into four main groups based mainly on their scratch numbers, although scratch texture has been useful in discerning a possible modern example of a C3 grazer (choushinga). Mixed feeders are separated into two main subgroups based on relative numbers of scratches, leading to a firmer understanding of the relative amounts of browse versus grass consumed by these taxa. The low-scratch mixed feeders are further differentiated by the relative fineness versus coarseness of scar features, opening the possibility of better understanding subtle differences in habitat and dietary partitioning in these animals. The finding that seasonal mixed feeders are similar to browsers when they browse, yet show differences in pit numbers and scratch range dispersion from grazers when they graze, is interesting and should be explored further.

The differentiation of seasonal and/or regional mixed feeders from meal-by-meal mixed feeders based on scratch numbers and scratch-range distributions has led to the interesting finding that meal-by-meal mixed feeding is not currently employed as a dietary strategy by mixed feeders in Africa (based on the ungulates included here), but is employed by Eurasian ungulates. These findings should lead to additional research into the potential reasons for such a disparity and for elucidating ungulate community structure. Also, insight should be provided into why meal-by-meal mixed feeders are more similar to grazers and high-abrasion feeders than to seasonal mixed feeders, with the latter being more similar to browsers and high-attrition feeders. Differences in the relative selectivity of food materials may explain some of these differences and may lead to further research along this line.

Important new evolutionary insights may also be gained from this work. The five-part scratch distribution sorting of extant taxa is a new finding which has shown that grazing may have evolved from meal-by-meal mixed feeding rather than directly from browsing or from mixed feeding, which varies regionally or seasonally. Also, scratch distribution patterns may offer insight into the expansion into new trophic zones by species. It is probable that browsing is more restrictive as a trophic strategy than is some form of grazing for enhancing the expansion of species into new habitats. Also, the idea that hypsodonty equals grazing needs to be revised based on this work. It is also evident that the crown height scenario might be more complicated than previously supposed. In addition, the simplified notion of the browsing-grazing transition in fossil horses is in serious need of revision. The theory that drier and cooler climatic shifts in the North American Miocene led to a rapid expansion of C4 grasslands, stimulating the transition of forest-browsing taxa directly into open habitat grazers, is unlikely to be valid based on this work. The idea of grazing evolving in forests on C3 grasses is much more likely as a first step in the widespread adoption of a grazing strategy in horses.

Finally, accuracy of the new methodology in correctly assigning known browsers, grazers, and mixed feeders to their correct trophic groups and the correspondence of microwear with mesowear results allay anxiety that the low-tech and rapid nature of this technique might dilute its effectiveness. In fact, due to the large sample sizes and increased faunal diversity involved in the new comparative database, more statistically significant results have been attained with the new technique than was previously possible. This has led to the modification of some traditional trophic group assignments for certain extant ungulates, and highlighted the need for further study of the dietary behavior of extant species.

The large and more eclectic new database developed here will be of use in future studies, not only for better understanding the nature of diets and habitats of fossil species, but also for stimulating further research into extant ungulate ecology.

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APPENDIX 1

Species Studied and Sources of Specimens

Taxon	Common name	Order	Family	Museum
Browsers				
Alces alces	moose	Artiodactyla	Cervidae	NMNH
Antilocapra americana	pronghorn	Artiodactyla	Antilocapridae	AMNH
Boocercus euryceros	bongo	Artiodactyla	Bovidae	AMNH
Budorcas taxicolor	takin	Artiodactyla	Bovidae	NHM, NMNH
Camelus bactrianus	bactrian camel	Artiodactyla	Camelidae	AMNH
Camelus dromedarius	dromedary	Artiodactyla	Camelidae	Field Museum
Capreolus capreolus	roe deer	Artiodactyla	Cervidae	NHM
Cephalophus natalensis	red forest duiker	Artiodactyla	Bovidae	AMNH
Cephalophus dorsalis	bay duiker	Artiodactyla	Bovidae	AMNH
Cephalophus niger	black duiker	Artiodactyla	Bovidae	AMNH
Cephalophus silvicultor	yellow-backed duiker	Artiodactyla	Bovidae	AMNH
Diceros bicornis	black rhinoceros	Perissodactyla	Rhinocerotidae	NMNH
Elephas maximus	Indian elephant	Proboscidea	Elephantidae	AMNH
Giraffa camelopardalis	giraffe	Artiodactyla	Giraffidae	NMNH, NMKenya
Litocranius walleri	gerenuk	Artiodactyla	Bovidae	AMNH
Loxodonta africana	African elephant	Proboscidea	Elephantidae	AMNH
Okapia johnstoni	okapi	Artiodactyla	Giraffidae	AMNH
Tapirus terrestris	S. American tapir	Perissodactyla	Tapiridae	NMNH
Tapirus bairdii	Baird's tapir	Perissodactyla	Tapiridae	NMNH
Tragelaphus imberbis	lesser kudu	Artiodactyla	Bovidae	AMNH, NMNH
Tragelaphus strepsiceros	greater kudu	Artiodactyla	Bovidae	AMNH, NMNH
Tragulus sp.	Asiatic mouse deer	Artiodactyla	Tragulidae	AMNH
Grazers				
Alcelaphus buselaphus	hartebeest	Artiodactyla	Bovidae	AMNH
Bison bison	Am. plains bison	Artiodactyla	Bovidae	AMNH, NMNH
Cervus duvauceli	barashingha	Artiodactyla	Cervidae	AMNH, NMNH
Connochaetes taurinus	wildebeest	Artiodactyla	Bovidae	NMNH
Equus burchelli	Burchell's zebra	Perissodactyla	Equidae	NMNH, NMKenya
Equus grevyi	Grevy's zebra	Perissodactyla	Equidae	NMNH
Hippotragus niger	sable antelope	Artiodactyla	Bovidae	AMNH, NMNH
Kobus ellipsipyrmnus	common waterbuck	Artiodactyla	Bovidae	AMNH
Tetracerus quadricornis	chousingha	Artiodactyla	Bovidae	NHM
Mixed feeders				
Axis axis	chital	Artiodactyla	Cervidae	AMNH, NMNH
Boselaphus tragocamelus	nilgai	Artiodactyla	Bovidae	NHM
Capra hircus	domestic goat	Artiodactyla	Bovidae	NMNH
Capra ibex	ibex	Artiodactyla	Bovidae	AMNH, NMNH
Capricornis sumatraensis	serow	Artiodactyla	Bovidae	AMNH, NMNH
Cervus unicolor	sambar	Artiodactyla	Cervidae	AMNH, NMNH
Cervus canadensis	wapiti	Artiodactyla	Cervidae	AMNH, NMNH
Gazella granti	Grant's gazelle	Artiodactyla	Bovidae	AMNH, NMNH
Gazella thomsoni	Thomson's gazelle	Artiodactyla	Bovidae	AMNH, NMNH, NMKenya
Hylochoerus mainerdjag	giant forest hog	Artiodactyla	Suidae	NMNH
Lama glama	llama	Artiodactyla	Camelidae	NMNH
Lama vicugna	vicugna	Artiodactyla	Camelidae	NMNH
Moschus moschiferus	musk deer	Artiodactyla	Moschidae	AMNH
Muntiacus muntjak	muntjac	Artiodactyla	Cervidae	NMNH
Ovibos moschatus	muskox	Artiodactyla	Bovidae	AMNH, NMNH
Ovis canadensis	bighorn sheep	Artiodactyla	Bovidae	NMNH
Potamochoerus porcus	African bush pig	Artiodactyla	Suidae	NMK

APPENDIX 1
Continued

Taxon	Common name	Order	Family	Museum
Mixed feeders (*continued*)				
Tragelaphus scriptus	bushbuck	Artiodactyla	Bovidae	AMNH, NMNH
Taurotragus oryx	eland	Artiodactyla	Bovidae	AMNH
Extinct Equidae				
Hyracotherium spp.		Perissodactyla	Equidae	AMNH, Ken Rose
Merychippus insignis		Perissodactyla	Equidae	AMNH
Mesohippus spp. mostly *M. bairdii*		Perissodactyla	Equidae	AMNH
Mesohippus hypostylus		Perissodactyla	Equidae	AMNH
Mesohippus westoni		Perissodactyla	Equidae	AMNH
Mesohippus-Miohippus		Perissodactyla	Equidae	AMNH
Parahippus spp.		Perissodactyla	Equidae	AMNH

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