AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3301, 36 pp., 26 figures, 4 tables October 16, 2000

Functional Characterization of Ungulate Molars Using the Abrasion-Attrition Wear Gradient: A New Method for Reconstructing Paleodiets

MIKAEL FORTELIUS[1] AND NIKOS SOLOUNIAS[2]

ABSTRACT

The analysis of fossil ungulate cheek teeth has long been one of the main sources of information about the terrestrial environments of the Cenozoic, but the methods used to extract this information have been either imprecise or prohibitively laborious. Here we present a method based on relative facet development that is quantitative, robust, and rapid. This method, which we term *mesowear analysis*, 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. Mesowear was recorded by examining the buccal apices of molar tooth cusps. Apices were characterized as sharp, rounded, or blunt, and the valleys between them either high or low. The method has been developed only for selenodont and trilophodont molars, but the principle is readily extendable to other crown types. Mesowear analysis is insensitive to wear stage as long as the very early and very late stages are excluded.

Cluster analysis of the mesowear variables produces clusters reflecting four main groups from abrasion-dominated to attrition-dominated: grazers, graze-dominated mixed feeders, browse-dominated mixed feeders, and browsers. Most of the relatively few apparent anomalies are explained by more detailed dietary information. Mesowear analysis provides resolution within the main dietary classes and the clustering is virtually identical with and without the index of hypsodonty. Discriminant analysis using all mesowear variables and hypsodonty

[1] Professor of Ecological Paleontology, Department of Geology, Division of Geology and Paleontology, PO Box 11 FIN-00014 University of Helsinki, Finland, mikael.fortelius@helsinki.fi

[2] Research Associate, Department of Paleontology, American Museum of Natural History and Associate Professor, Department of Anatomy, New York College of Osteopathic Medicine, New York Institute of Technology, Old Westbury, NY 11568 8000 USA, nsolouni@iris.nyit.edu

Copyright © American Museum of Natural History 2000 ISSN 0003-0082 / Price $4.50

showed an overall correct classification of 76% of 64 species of living ungulates into the conventional dietary categories of browser, grazer, and mixed feeder, while a smaller set of 27 ''typical'' species was correctly classified at 96%. Alternative ''conservative'' and ''radical'' dietary classifications that were employed to accommodate cases where dietary information was controversial or unclear produced only marginally different results. Mesowear analysis successfully resolved a test case using the Serengeti grazing succession and appears to be superior to microwear analysis in two cases where the diet of fossil ungulates has been previously studied by microwear and other conventional methods.

INTRODUCTION

Because of their ubiquity and close relationship to understandable physical and biological relationships, fossil herbivore teeth are commonly used to reconstruct the diet and environment of extinct species. The main limitation so far has been the fact that detailed and reliable dietary interpretation from mammalian herbivore teeth has involved expensive, laborious, and time-consuming methods, which have made it difficult to apply them to more than a few species from a limited number of localities (e.g., Rensberger, 1973; Fortelius, 1982; Rensberger et al., 1984; Teaford and Walker, 1984; Fortelius, 1985; Janis and Fortelius, 1988; Janis, 1990; Solounias and Moelleken, 1992a, 1992b; Solounias and Hayek, 1993; Hunter and Fortelius, 1994; Solounias et al., 1994, 1995). We present a greatly simplified procedure for rapidly characterizing the major (selenodont and trilophodont) morphological types of molar teeth found among Cenozoic large mammalian herbivores in relationship to a functional and ecological framework. The ultimate purpose is to develop a reliable and inexpensive method to rapidly analyze large numbers of extinct taxa in museums so that entire ungulate paleocommunities may be studied effectively.

The dietary interpretation of mammalian teeth has traditionally involved either direct (actualistic) comparison with living animals, the application of general functional principles, or—increasingly during the latest few decades—the study of the wear patterns left on teeth by food. The distinction between these approaches is somewhat blurred, however, for most actualistic comparisons since Cuvier, have in fact contained a functional element (Van Valkenburgh et al., 1990), and wear patterns are almost unavoidably included in any morphological comparison of teeth. Perhaps a more satisfactory grouping could be based on the time scale involved: the unworn (preformed) morphology of the tooth reflects evolution in deep geological time, the wear pattern visible to the naked eye (or preferably low magnification) reflects a substantial portion of the individual's life in ecological time, and the microscopically visible details (microwear) reflect a time that is short even in comparison with the individual's life span. None of the levels is inherently more important than the others, but each answers somewhat different questions; considering each level separately will improve functional interpretation.

The unworn morphology, expressed for example in classic terms such as hypsodont or lophodont, reflects long-term adaptation and sets the main mechanical constraints on what foods an individual can hope to successfully utilize. Masticatory morphology, hypsodonty, tooth structure and enamel structure belong to the preformed adaptations in deep time. The information provided by preformed morphology is too general, however, to resolve morphologically homogeneous groups such as the selenodont artiodactyls (e.g., Jernvall et al., 1996). At the other extreme, microwear provides direct information about the nature of the last few to several meals of an individual (Solounias et al., 1994; Teaford and Oyen, 1989).

In many ways it is the intermediate level, which we term mesowear, that seems to offer the best hope for answering questions relating to the average diet of a particular species from a particular location in space and time (fig. 1). Mesowear patterns are best described in terms of facet development (Butler, 1952; Janis, 1990), and best understood as the combined result of both attrition and abrasion, i.e., the relative contributions of tooth-on-tooth and food-on-tooth wear (Butler, 1972;

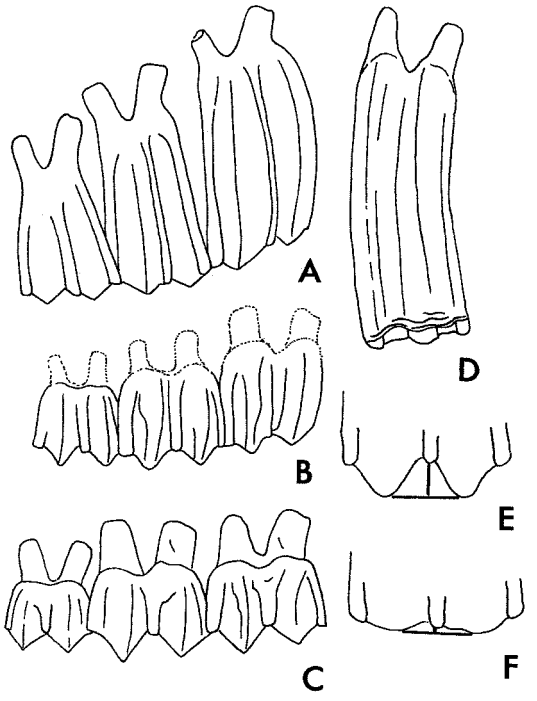

Fig. 1. Mesowear features used in this study and a sample of hypsodont, mesodont, and brachydont teeth. **A**. *Capra hircus*, goat, Basel Museum 3379 (tooth relief high and cusps sharp). **B**. *Cervus duvaucelli* AMNH 54498 (mesodont, tooth relief high and cusps rounded). **C**. *Odocoileus virginianus*, white tailed deer, Canadian Royal Museum Toronto 2091 (brachydont, tooth relief high and cusps sharp). **D**. *Equus caballus*, domestic horse personal collection (hyperhypsodont, tooth relief low and cups blunt; actually concave and thus blunter than other grazers do). **E**. *Kobus ellipsiprymnus* (NS, personal collection) (tooth relief high and cups rounded). **F**. *Alcelaphus buselaphus* (NS, personal collection) (tooth relief low and cusps blunt). Height of relief is shown in relation to the actual length of cusps.

Fortelius, 1985). The fibrous, nonbrittle plant foods that make up the diet of most selenodont and lophodont ungulates can only be cut when the cutting edges push clean through the food, so that the occluding dental facets come into direct contact (Rensberger, 1973; Lucas, 1979; Walker, 1984). This means that direct tooth-on-tooth wear (attrition) will always occur in these forms, a fact that explains why precise occlusion between upper and lower teeth is maintained until the very latest wear stages even in species where the attrition signal is partly or completely masked by abrasion. Mesowear is best observed with the naked eye or at low magnification, for example with a hand lens. It affects all occlusal surfaces of teeth but in the present study we restrict our observations to the buccal edges of the paracones and metacones of upper molars as two variables observable from the buccal side: cusp relief and cusp shape.

Cusp relief is to the relative difference in height between cusp tips and inter cusp valleys as seen in buccal projection, i.e., how high the cusps appear in lateral view. We will show that there is strong empirical evidence that the combination of absolutely high attrition and abrasion, as seen in extreme grazers, results in low occlusal relief. The theoretical explanation for this relationship remains somewhat obscure but the high relief typically seen in ''fresh grass'' grazers, like *Kobus ellipsiprymnus* or *Redunca redunca*, suggests that lower occlusal stress permits a higher occlusal relief to develop.

Cusp shape refers to the apex of the cusp (here paracone or metacone) described as sharp, rounded, or blunt, in decreasing order of facet development. The theoretical basis is easily understood in terms of the relative contribution of attrition and abrasion to the total wear: sharp cusps mean that attrition predominates strongly, whereas the attrition signal is almost completely masked by abrasion in blunt cusps.

The ordinary dental wear visible to the naked eye or at low magnification has not been a favorite target of research among mammalian paleontologists. Every (1970) and Every and Kühne (1971) attributed attritional wear to ''thegosis,'' or the active sharpening of teeth not associated with chewing food. There seems to be no evidence for such behavior, however, nor any need to invoke it to explain dental wear patterns (Osborn and Lumsden, 1978). More relevant to the present purpose, Guthrie (1990) reported differences in the teeth of bison between sedge-eating and grass-eating individuals, and Janis (1990) used mapping of ''gross dental wear'' to deduce diet in fossil mammals, based on comparison with Recent species. The method we describe here uses the same principle, stripped to its barest essentials.

TABLE 1
Species Studied and Summary Statistics
For abbreviations see appendix.

Order	Family	Common name		Class	N	cons	radi	jad1	jad2	hyp	hyp-ind	per-high	per-sharp	per-round	per-blunt
			Browsers (conservative)												
Artiodactyla	Cervidae	moose	*Alces alces* (AA)	ty	30	B	B	H	B	b	1.34	100.0	100.0	0.0	0.0
Artiodactyla	Bovidae	dibatag	*Ammodorcas clarkei* (EI)	no	7	B	B	H	B	b	2.23	100.0	28.5	71.4	0.0
Artiodactyla	Antilocapridae	pronghorn	*Antilocapra americana* (AM)	no	44	B	B	M	M	h	4.61	96.0	88.6	11.3	0.0
Artiodactyla	Bovidae	bongo	*Boocercus euryceros* (BE)	no	27	B	B	B	B	b	1.92	100.0	44.4	55.5	0.0
Artiodactyla	Cervidae	roe deer	*Capreolus capreolus* (OL)	no	68	B	B	W	M	b	1.49	96.0	72.0	25.0	2.9
Artiodactyla	Bovidae	bay duiker	*Cephalophus dorsalis* (DR)	mb	28	B	B	S	B	b	1.15	93.0	32.1	60.7	7.1
Artiodactyla	Bovidae	red forest duiker	*Cephalophus natalensis* (NA)	mb	6	B	B			b		100.0	16.6	83.3	0.0
Artiodactyla	Bovidae	black duiker	*Cephalophus niger* (NI)	mb	31	B	B			b		91.0	35.4	61.2	3.2
Artiodactyla	Bovidae	black-fronted duiker	*Cephalophus nigrifrons* (NI)	mb	44	B	B			b		82.0	25.0	70.4	4.5
Artiodactyla	Bovidae	yellow-backed duiker	*Cephalophus silvicultor* (SL)	mb	39	B	B	B	B	b	2.23	80.0	0.0	94.8	5.1
Hyracoidea	Procaviidae	southern tree hyrax	*Dendrohyrax arboreus* (DA)	mb	20	B	B			b		100.0	50.0	50.0	0.0
Hyracoidea	Procaviidae	western tree hyrax	*Dendrohyrax dorsalis* (DD)	mb	28	B	B	H	B	b	1.53	82.0	46.4	53.5	0.0
Perissodactyla	Rhinocerotidae	Sumatran rhinoceros	*Dicerorhinus sumatrensis* (DS)	ty	5	B	B	B	B	b	1.67	100.0	80.0	20.0	0.0
Perissodactyla	Rhinocerotidae	black rhinoceros	*Diceros bicornis* (DB)	ty	34	B	B	B	B	m	2.24	100.0	94.1	5.8	0.0
Artiodactyla	Giraffidae	giraffe	*Giraffa camelopardalis* (GC)	ty	61	B	B	H	B	b	1.20	94.0	73.7	26.2	0.0
Hyracoidea	Procaviidae	Bruce's yellow spotted hyrax	*Heterohyrax brucei* (HB)	mb	11	B	B			b		36.0	81.8	18.1	0.0
Artiodactyla	Tragulidae	water chevrotain	*Hyaemoschus aquaticus* (HY)	mb	18	B	B	S	B	b	1.30	100.0	16.6	83.3	0.0
Artiodactyla	Bovidae	gerenuk	*Litocranius walleri* (LW)	no	69	B	B	H	B	b	1.32	96.0	33.3	66.6	0.0
Artiodactyla	Cervidae	mule deer	*Odocoileus hemionus* (OH)	ty	33	B	B	B	B	b	1.59	100.0	72.7	27.2	0.0
Artiodactyla	Cervidae	white-tailed deer	*Odocoileus virginianus* (OV)	ty	18	B	B	B	B	b	1.23	100.0	88.8	11.1	0.0
Artiodactyla	Giraffidae	okapi	*Okapia johnstoni* (OJ)	ty	8	B	B	H	B	b	1.18	100.0	87.5	12.5	0.0
Perissodactyla	Rhinocerotidae	Javan rhinoceros	*Rhinoceros sondaicus* (RS)	ty	5	B	B	B	B	b	1.72	100.0	100.0	0.0	0.0
Artiodactyla	Bovidae	greater kudu	*Tragelaphus strepsiceros* (TS)	no	7	B	B	B	B	b	2.29	100.0	0.0	100.0	0.0
			Grazers (conservative)												
Artiodactyla	Bovidae	hartebeest	*Alcelaphus buselaphus* (ab)	ty	76	G	G	G	G	h	5.23	57.0	3.2	66.6	28.0
Artiodactyla	Bovidae	Lichtenstein's hartebeest	*Alcelaphus lichtensteinii* (al)	no	17	G	G			h		82.0	5.8	82.3	11.7
Artiodactyla	Bovidae	American plains bison	*Bison bison* (bb)	ty	15	G	G	G	G	h	4.87	0.0	0.0	26.6	73.3
Perissodactyla	Rhinocerotidae	white rhinoceros	*Ceratotherium simum* (cs)	ty	26	G	G	G	G	h	3.09	0.0	0.0	72.0	28.0
Artiodactyla	Bovidae	wildebeest	*Connochaetes taurinus* (ct)	ty	52	G	G	G	G	h	4.94	55.0	15.3	55.7	28.8
Artiodactyla	Bovidae	topi	*Damaliscus lunatus* (dl)	ty	5	G	G	G	G	h	5.10	20.0	20.0	60.0	20.0
Perissodactyla	Equidae	Burchell's zebra	*Equus burchelli* (eb)	ty	122	G	G	G	G	h	5.83	0.0	27.0	39.3	33.6
Perissodactyla	Equidae	Grevy's zebra	*Equus grevyi* (eg)	ty	29	G	G	G	G	h	5.80	0.0	34.4	41.3	24.1
Artiodactyla	Bovidae	roan antelope	*Hippotragus equinus* (he)	ty	26	G	G	G	G	h	4.28	85.0	3.8	96.1	0.0
Artiodactyla	Bovidae	sable antelope	*Hippotragus niger* (hn)	ty	20	G	G	G	G	h	3.77	85.0	0.0	85.0	15.0
Artiodactyla	Bovidae	common waterbuck	*Kobus ellipsiprymnus* (ke)	ty	22	G	G	F	G	h	3.47	96.0	0.0	100.0	0.0
Artiodactyla	Bovidae	bohor reedbuck	*Redunca redunca* (rr)	ty	77	G	G	F	G	h		91.0	6.4	90.9	2.5

TABLE 1
Continued

Order	Family	Common name		Class	N	cons	radi	jad1	jad2	hyp	hyp-ind	per-high	per-sharp	per-round	per-blunt
			Mixed feeders (conservative)												
Artiodactyla	Bovidae	impala	*Aepyceros melampus* (Me)	ty	17	M	M	M	M	h	4.89	100.0	35.2	64.7	0.0
Artiodactyla	Bovidae	springbuck	*Antidorcas marsupialis* (Ma)	no	26	M	M	M	M	m	4.89	96.0	73.0	26.9	0.0
Artiodactyla	Cervidae	chital	*Axis axis* (Ax)	no	43	M	G			m		79.0	6.9	67.4	25.5
Artiodactyla	Cervidae	hog deer	*Axis porcinus* (Ap)	no	24	M	G	M	M	m	2.53	88.0	4.1	95.8	0.0
Artiodactyla	Bovidae	nilgai	*Boselaphus tragocamelus* (Tr)	no	15	M	M	W	M	m	3.03	87.0	0.0	100.0	0.0
Artiodactyla	Bovidae	takin	*Budorcas taxicolor* (Bt)	no	38	M	B	M	M	h	3.43	95.0	42.1	57.8	0.0
Artiodactyla	Camelidae	dromedary	*Camelus dromedarius* (Cl)	no	16	M	B	M	M	h	2.52	100.0	31.2	68.7	0.0
Artiodactyla	Bovidae	ibex	*Capra ibex* (Ci)	no	24	M	M	M	M	h	4.71	97.0	54.1	37.5	8.3
Artiodactyla	Bovidae	serow	*Carpicornis sumatraensis* (Cs)	ty	22	M	M	M	M	h	3.93	100.0	45.4	50.0	4.5
Artiodactyla	Cervidae	wapiti	*Cervus canadensis* (Cc)	ty	19	M	M	W	M	b	1.96	100.0	47.3	52.6	0.0
Artiodactyla	Cervidae	barashingha	*Cervus duvauceli* (Cd)	no	50	M	G			m		67.0	12.0	64.0	24.0
Artiodactyla	Cervidae	sambar	*Cervus unicolor* (Cu)	no	21	M	M	W	M	m	2.20	91.0	14.2	80.9	4.7
Artiodactyla	Bovidae	Grant's gazelle	*Gazella granti* (Gg)	ty	18	M	M	M	M	h	3.45	88.0	50.0	50.0	0.0
Artiodactyla	Bovidae	Thomson's gazelle	*Gazella thomsoni* (Gt)	ty	146	M	M	M	M	h	3.77	88.0	55.4	43.1	1.3
Artiodactyla	Camelidae	llama	*Lama glama* (Lg)	no	32	M	M			h		100.0	28.1	68.7	3.1
Artiodactyla	Camelidae	vicugna	*Lama vicugna* (Lv)	no	12	M	M	M	M	h	4.33	100.0	41.6	58.3	0.0
Artiodactyla	Bovidae	oribi	*Ourebia ourebi* (Oo)	no	128	M	G	M	M	h	3.80	96.0	21.8	77.3	0.7
Artiodactyla	Bovidae	muskox	*Ovibos moschatus* (Om)	ty	52	M	M	M	M	h	3.69	81.0	57.6	42.3	0.0
Artiodactyla	Bovidae	bighorn sheep	*Ovis canadensis* (Oc)	no	31	M	M	M	M	h	4.11	87.0	48.3	51.6	0.0
Hyracoidea	Procaviidae	rock hyrax	*Procavia capensis* (Pc)	mb	24	M	M	G	G	b	1.69	46.0	62.5	37.5	0.0
Artiodactyla	Bovidae	mountain reedbuck	*Redunca fulvorufula* (Rf)	no	7	M	G	M	M	h	3.79	86.0	0.0	100.0	0.0
Perissodactyla	Rhinocerotidae	Indian rhinoceros	*Rhinoceros unicornis* (Ru)	no	5	M	M	W	M	b	1.59	100.0	80.0	20.0	0.0
Artiodactyla	Bovidae	saiga	*Saiga tatarica* (St)	no	5	M	M	M	M	h	5.29	40.0	60.0	40.0	0.0
Artiodactyla	Bovidae	African buffalo	*Syncerus caffer* (Sc)	no	31	M	G	M	M	h	3.00	100.0	0.0	93.5	6.4
Artiodactyla	Bovidae	eland	*Taurotragus oryx* (To)	ty	14	M	M	M	M	m	2.91	100.0	50.0	50.0	0.0
Artiodactyla	Bovidae	chousingha	*Tetracerus quadricornis* (Tq)	no	21	M	G	W	M	m	2.89	91.0	28.5	71.4	0.0
Artiodactyla	Bovidae	nyala	*Tragelaphus angasi* (Ta)	no	20	M	B	W	M	b	2.52	100.0	35.0	65.0	0.0
Artiodactyla	Bovidae	lesser kudu	*Tragelaphus imberbis* (Ti)	no	31	M	B	W	M	b	1.97	100.0	61.2	38.7	0.0
Artiodactyla	Bovidae	bushbuck	*Tragelaphus scriptus* (Ts)	ty	47	M	M	W	M	b	2.54	100.0	51.0	48.9	0.0
			Extinct species												
Perissodactyla	Equidae		*Cormohipparion goorisi* (cG)	fo	17					h		100.0	0.0	100.0	0.0
Perissodactyla	Equidae		*Cormohipparion quinni* (cQ)	fo	13					h		94.0	20.0	80.0	0.0
Perissodactyla	Equidae		*Cremohipparion proboscideum* (cP)	fo	8					h		100.0	75.0	25.0	0.0
Perissodactyla	Equidae		*Merychippus insignis* (mI)	fo	27					m		96.0	28.6	67.9	3.6
Artiodactyla	Bovidae		*Pachytragus crassiciornis* (pR)	fo	24					m		100.0	30.0	70.0	0.0
Artiodactyla	Bovidae		*Pachytragus laticeps* (pL)	fo	40					m		100.0	62.5	37.5	0.0

TABLE 2
Effect of Age or Wear Stage on Mesowear When Age Is Known and Sample Is Relatively Large

Species	Age	N	High (%)	Low (%)	Sharp (%)	Rounded (%)	Blunt (%)
Rangifer tarandus caribou	49–51 months	10	10 (100)	0	8 (80)	2 (20)	0
	61–77 months	16	16 (100)	0	14 (87)	2 (12)	0
	85–97 months	10	10 (100)	0	7 (70)	3 (30)	0
Gazella thompsoni Thomson's gazelle	young	7	7 (100)	0	5 (71)	2 (28)	0
	young adult	24	24 (100)	0	20 (83)	4 (16)	0
	older adult	7	7 (100)	2 (28)	2 (28)	3 (42)	0
Cephalophus nigrifrons black-fronted duiker	young	7	7 (100)	0	3 (42)	4 (57)	0
	young adult	6	6 (100)	0	4 (66)	2 (33)	0
	older adult	10	10 (100)	0	1 (10)	9 (90)	0
	old	3	2 (66)	1 (33)	1 (33)	1 (33)	1 (33)
Equus burchelli plains zebra	2–5 years	3	0	3 (100)	0	0	3 (100)
	5–9 years	4	0	4 (100)	0	0	4 (100)
	9–13 years	3	0	4 (100)	0	0	4 (100)
Tragelaphus scriptus bushbuck	young adult	4	4 (100)	0	3 (75)	1 (25)	0
	older adult	5	5 (100)	0	4 (80)	1 (20)	0
Redunca redunca reedbuck	young adult	2	2 (100)	0	0	2 (100)	0
	older adult	2	2 (100)	0	0	2 (100)	0
Syncerus caffer African buffalo	adult	3	3 (100)	0	0	3 (100)	0

MATERIALS

We used extant species to develop the new mesowear analysis and we tested the method with both extant and extinct species. A sample of extant ungulate species was used to examine the stability of mesowear during ontogeny (mesowear stability test) for a test case using the Serengeti grazing succession and for two pilot applications on fossil equids and bovids.

DATABASE

A comparative database was developed for 2200 individuals representing upper molar teeth from 64 extant ungulate species (table 1). The material was studied in the mammalogy collections of several museums (see Acknowledgments). The variables included in table 1 are explained below and under Methods. The raw data are available on request from either author.

SAMPLES FOR MESOWEAR STABILITY TEST

Mesowear analysis is applicable only if factors related to diet have a significantly stronger influence on wear patterns than factors related to structure or wear stage. The former problem is addressed by the present study as a whole, but the latter requires special attention. It was surprisingly difficult to find large populations of individuals of well-known age to investigate the effect of wear stage. We were able, however, to study a population of 36 reindeer from Canada (a personal collection) for which age is known from annuli in the lower first molar roots (see Solounias et al., 1994, for more details) (table 2). Individuals from six additional species were selected (table 2): the plains zebra aged by the degree of incisor wear (following methods of Bone, 1964; Klingel, 1965; Slade and Godfrey, 1982) omson's gazelle, bohor reedbuck, bushbuck, and black-fronted duiker by number of keratinous rings on horns, size of horns, and second molar height; and African buffalo by size and curvature of horns (following a study for the springbuck, Rautenbach 1971).

UNGULATE DIETS—DERIVING TABLE 1

Several factors can complicate the relationship of diets to morphology in extant species. Although investigators who study the evolution and adaptation of ungulates have related morphology to reported diets

(e.g., Webb, 1983; Fortelius, 1985; Janis, 1988; Solounias et al., 1994), it is clear that diets reported in the literature are often based on small samples from single populations, and that diet would be best studied by extensive field observation or fecal collections. Many ungulates are also opportunistic, and their diets vary by place and by season, so that what can be observed for a few years and in certain places may not hold for the thousands to millions of years that a particular species existed. We acknowledge that dietary information for Recent species is often less than perfect but cannot suggest any immediate remedy. Furthermore, for the method presented here, even a rough classification based on physical properties of plant foods would be preferable to one based on systematics or general appearance.

General dietary classes (browser, grazer, mixed feeder) are problematic for two reasons. They lump a diversity of foods and lifestyles under three broad categories, and scientists have used different definitions for them, not often explicitly stated. However, these dietary classes are so firmly entrenched in the literature that any new approach must somehow relate back to them. Although our study emphasizes a continuum—a spectrum of diets based on their mechanical (wear) properties in terms of abrasion and attrition—we have chosen this general classification as the base against which to compare the results of this study. We use the conventional 90% cutoff points to define the classes: browsers take $<10\%$ grass, grazers $<10\%$ browse. The huge spectrum between these extremes is lumped into the obviously heterogeneous mixed feeder category.

Table 1 lists the basic dietary classifications compiled from Janis (1988) and several other sources (in particular: Tener, 1965; Schaller, 1967; Hofmann, 1973; Labâo-Tello and Van Gelder, 1975; Schaller, 1977; Sinclair, 1977; Gauthier-Pilters and Dagg, 1981; McDonald, 1981; Chapman and Feldhammer, 1982; Kingdon, 1982a; 1982b; Nowak and Paradiso, 1983; Hofmann, 1985; Schaller et al., 1986; Hofmann, 1989; Nowak, 1991). In recognition of some uncertainty and ambiguity we have used two parallel classifications of our 64 species: a ''conservative'' classification (cons) where doubtful cases are treated as intermediate (mixed feeder) and a ''radical'' classification (radi) where such cases are treated as extreme (browser or grazer). Comparison of results from the two classifications enables us to gauge the effect of such subjective choices and to evaluate their impact on the results. The variable Jad1 gives the diet as reported by Janis (1988); Jad2 gives the corresponding value translated to the simple browser-grazer-mixed feeder classification. Our conservative dietary classification differs from that of Janis (1988) for three species: *Antilocapra americana*, *Capreolus capreolus*, and *Procavia capensis*, but agrees with the present opinion of Dr. Janis (personal commun., July 1999). Table 1 also features the ad hoc classifying variable Class, with four values: fo (fossil), no (no particular class), mb (''mabra,'' minute abraded brachydont, identified under Results, Cluster Analysis), and ty (typical of its dietary class).

Test Case: A known Dietary Succession in the Serengeti

We tested this method on a grazing succession from the Serengeti (Bell, 1971), involving plains zebra, topi, wildebeest, and sometimes the hartebeest and Thomson's gazelle. Bell observed that 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. Finally, the gazelle follows, feeding on the smallest and softest vegetation. The precise sequence of this succession is essential for these species to find their required vegetation. We predict that the mesowear will replicate this succession such that the zebra and the gazelle will bracket the other three species.

Fossil Samples

Fossil Bovids: *Pachytragus laticeps* and *Pachytragus crassicornis* are two species of early Caprini (Bovidae) from the Miocene of Samos collected by Brown in 1924 (Gentry, 1971; Solounias, 1981). *P. laticeps* has longer and more backwardly curved horn cores than *P. crassicornis*, which is also smaller and has a more posteriorly placed toothrow (Gentry, 1971). Based on general consider-

ation of the cranial morphology and dentition, Gentry (1971) suggested that *P. crassicornis* was more advanced and adapted to a harsher environment than *P. laticeps*. In contrast, Solounias and Moelleken (1992b) determined from a tooth microwear analysis that *P. laticeps* was a grazer and *P. crassicornis* a mixed feeder. Based on masseter attachment morphology and using the morphology of the masseter muscle attachments, Solounias et al. (1995) concluded that both species were mixed feeders and suggested that *P. laticeps* was further removed from the browsing mode than *P. crassicornis*. We have collected mesowear data for these species to see whether this problem can be resolved.

FOSSIL EQUIDS: Hayek et al. (1992) used microwear to study the paleodiet of the following fossil equids: *Mesohippus insignis* from the Olcott Formation of Nebraska, *Cormohipparion goorisi* from Trinity River Pit, Flemming Formation, Cold Springs Texas, *Cormohipparion quinni* (formerly *C. sphenodus)*, from Valentine Formation, Cornell Dam Member Nebraska, and *Cremohipparion proboscideum* Quarry 1 of Samos, Greece (Sondaar, 1971). We have collected mesowear data from the same populations in order to compare the results obtained by the two techniques.

All fossil samples were from the Division of Paleontology of the American Museum of Natural History (New York).

METHODS

SCORING ROUTINES FOR MESOWEAR

Although additional mesowear features can be defined (a larger and more detailed study is in progress), the present study bases mesowear on two variables: occlusal relief and cusp shape (fig. 1). Ungulate teeth were inspected at close range, using a hand lens when appropriate. The first several hundred specimens were photographed and traced on paper, but once the standards had been set to our satisfaction the rest of the material was recorded by direct scoring. We provide several figures, simple outlines of molars, which show the buccal outlines of a selection ungulate teeth illustrating the various morphologies. Artistic shadow has not been included in order to emphasize the shape of the tooth outlines. Parallax due to photography was ignored as we only scored qualitatively three general categories. We only used specimens in which the last molar was in occlusion and the first molar retained an occlusal shape similar to the second molar. Consequently, the effect of age was minimized, as discussed further under Results. After experimenting with various choices and standards, we settled on the sharper buccal cusp of the second upper molar; that is, either the paracone or metacone. This was done for simplicity, and we would like to stress that our experience strongly indicates that the choice of molar buccal cusp is not critical. (For example, the paracone and metacone are usually identical in mesowear of a single individual.) The selection of the sharpest cusp will drive the data slightly toward sharpness. This is a conservative decision, since after the very first wear stage, sharpness is never an artifact of wear stage, whereas blunting may be so.

Occlusal relief was classified as high or low, depending on how high the cusps rise above the valley between them (fig. 1). After some practice, simple scoring is sufficient, but in borderline cases a quantitative index can be constructed as follows. The buccal profile of the tooth is projected onto a plane. The vertical distance between a line connecting two adjacent cusp tips and two adjacent valley bottoms is measured, and divided by the length of the whole tooth (fig. 1). For selenodont forms and plagiolophodont equids, the limit between high and low was arbitrarily set at 0.1, for hyracoids at 0.05, and for rhinoceroses at 0.03. These values were calibrated by the relief observed in the species included in the study, to separate the subjectively ''low'' from the subjectively ''high.'' Negative relief (cusp tip lower than sides) was sometimes seen in hypsodont equids, and was treated as low. The progressive blunting of a cusp (see below) will inevitably reduce occlusal relief. That is to say, cusp shape and relief are not entirely independent, but converge at the low and blunt (''grazer'') end of the spectrum. We included occlusal relief, anticipating its usefulness for the study of fossil forms, particularly nongrazing hypsodont plagiolophodonts, which include many hipparions. Occlusal relief is

used in the analyses as a percentage and is given in table 1 as percent of high relief (perhigh).

Cusp shape was scored as sharp, rounded, or blunt (fig. 1, table 1) according to the degree of facet development. A sharp cusp has (practically) no rounded area between the mesial and distal phase I facets, a rounded cusp has a distinctly rounded tip without planar facet wear but retains facets on the lower slopes, while a blunt cusp lacks distinct facets altogether. Cusp shape is also used as a percentage and is given in table 1 as three variables: persharp, perround, and perblunt.

Dental structure and phylogenetic history obviously influence both occlusal relief and cusp shape. The blunt cusps of true Bovini and the low occlusal relief of present-day horses are at least partly the result of obvious structural modifications of the teeth. Apart from calibrating the cut-off points for high and low relief for individual groups as explained above, we have not attempted to correct for these influences here, although this may later become necessary. It is our contention that these differences are due to adaptive evolution and largely follow the pattern established by mesowear. They appear to amplify rather than disguise the mesowear signal, and are therefore not a problem unless the resolution desired is very high. A brief ''how to do it'' description of mesowear analysis is given within Methods.

Hypsodonty

The goal of our study is to develop a method for the dietary interpretation of extinct species, and the currently best established gross morphological predictor of diet in ungulates is hypsodonty (Janis, 1988), the main aspect of functional durability in the face of wear (Janis and Fortelius, 1988). Hypsodonty must obviously be included in our study, but is perhaps best conceived of as a proxy for overall wear rate (Solounias et al., 1994), rather than as a morphological character as such, just as the mesowear variables are conceived as proxies for kinds of wear.

In deciphering extinct species, the degree of hypsodonty can usefully be employed to select an appropriate subset of extant species for comparison. The logic here is simply that the relationship between attrition and abrasion is studied separately for different total wear regimes. However, for the cluster and discriminant analyses, all crown heights were considered together.

Hypsodonty indices (table 1, hypind) were taken from Janis (1988): width divided by the length of third lower molar (cement has been excluded in these measurements). For convenience, the species were partitioned into the conventional categories: brachydont (b), mesodont (m) or hypsodont (h). With such a tripartite subdivision, the hypsodonty of most taxa can be readily determined by observation. It is primarily the mesodont species and those on the borderlines that need to be measured or carefully examined for correct assignment. Mesodont artiodactyls are those with indices between 2.6 and 3.4 and all perissodactyls and hyraxes with indices between 2.0 and 3.0. Brachydont artiodactyls have indices of 2.5 or lower, and hypsodonts have indices of 3.5 or lower (table 1, hyp). The camel was classified as hypsodont despite the unexpectedly low index reported by Janis (1988), but the index reported was used in the analyses. Hog deer, Grant's gazelle, nyala, and the bushbuck are all just below our limit for mesodonts. The takin, Thomson's gazelle, and the common waterbuck are all just above our limit for hypsodonts. Figure 1 shows examples of brachydont, mesodont, and hypsodont teeth.

Statistical Analyses

The significance of differences observed in simple comparisons was tested using the Kruskal-Wallis test and the chi square test, as appropriate. Hierarchical cluster analysis was performed for several sets of species, with Euclidean distance and complete linkage (to enhance the distinctness of clusters), using three mesowear variables with and without the index of hypsodonty. Three of the four mesowear variables are percentages of cusp sharpness and add up to 100; therefore a maximum of two of those were included for any analysis). Discriminant analysis was performed for single variables and for all combinations of the mesowear variables plus the index of hypsodonty, using two dietary clas-

sifications (conservative and radical) alternately as grouping variable. We report the percentage of correct classifications from the jackknifed classification matrix (table 3). All statistical tests were performed on Systat 7.0 in a PC environment, using the default settings except where noted.

Practicalities of Mesowear Data Collection and Analysis

Since this paper is intended to introduce an easy and generally applicable method of paleodiet reconstruction we agree with one of our reviewers (Dr. R. L. Bernor) that a ''cookbook'' section is warranted.

The first step in mesowear analysis is obviously to obtain the material. It is important to select the specimens such that teeth in very early and very late wear are excluded, and to avoid scoring the shape of cusps that are either damaged or modified by structural elements (like the paracone of a rhinoceros). Pilot studies have revealed that lower teeth consistently score more rounded than do uppers, and we suggest that the two should not be mixed. Using lower teeth requires building up a comparative sample of lower teeth. We used only uppers in this paper. A sample of less than ten specimens should be treated with caution, while more than 30 is probably excessive.

The scoring procedure itself is described in the method section of this paper and is not repeated here. There is no doubt that it can be refined, but care should be taken not to loose the generality of the method, since restricting it to a single, morphologically uniform group will severely limit the choice of recent species available for comparison. Several of our figures are intended as an aide for scoring. Once the mesowear data exist as a file they can be analyzed by appropriate statistical means (we are sure that both our choice and our application of methods can be improved upon!). The raw data allow comparisons between pairs or groups of species using (for example) the chi square test, while the discriminant and cluster analyses require summary data in the form of (for example) percentages of occlusal relief and cusp shape values.

Blind reliance on statistics is to be discouraged, for reasons exemplified by the ''mabra-syndrome'' identified in this paper. An important part of more detailed mesowear analyses than those reported here will be the selection of the appropriate comparative sample, much as one would do for estimating body mass by regression techniques. It would clearly not be wise to analyze a small and brachydont species in relation to a sample of large and hypsodont ones, for example. The figures of teeth in this study are offered as an aide to make a first rough assessment of the general mesowear regime of a sample.

RESULTS

Stability of Relief and Cusp Shape During Wear

Reindeer Specimens: Ten young specimens (49–51 months) showed a high consistency with 80% sharp cusps. The 16 older individuals (61–77 months) had 87% sharp cusps and 12% rounded. The oldest 10 individuals, ranging 85–97 months, had 70% sharp and 30% rounded cusps. All specimens were high in relief. Chi square tests of the three groups gave low probabilities that the three age classes are different from each other (p values ranged from 0. 552 to 0.187). We conclude that, although there is some increase in roundedness with wear, the mesowear signature is nevertheless reasonably maintained throughout an individual's life (table 2).

Six additional species were also selected for the study of ontogenetic effects on the occlusal relief and cusp shape. All species showed that these parameters remain relatively stable from early middle wear until advanced age. In 24 Thomson's gazelles with 17 to 23 horn rings 83% of cusps were sharp. Seven younger individuals had 71% sharp cusps, while in 7 older individuals 29% of cusps were sharp. In the black-fronted duiker, the proportions of cusp shape (in this case, sharp and rounded) are reasonably stable throughout the life span of the individuals studied (table 2). Low relief and blunt cusps were found in 11 individuals of plains zebra spanning 2–13 years (aged by incisor wear stages), showing that the bluntness is genuinely present in early as well as late wear.

TABLE 3
Percentage Correctly Classified Cases (Jackknifed Matrix) in Discriminant Analysis of Groups of Species
Data are reported for all Recent species, for all without mabra, and for typical species.

Dietary classification	All Recent		Without mabra			
	Cons	Radi	Cons	Radi	Typical[a]	Mean
Single-variable						
persharp	47	56	61	69	96	66
perround	34	52	48	59	81	55
perblunt	48	58	48	61	67	56
perhigh	55	56	56	56	63	57
hypind	65	59	63	57	81	65
Mean	50	56	55	60	78	60
Two-variable						
hypind + persharp	76	76	76	73	96	79
hypind + perround	63	67	65	67	88	70
hypind + perblunt	80	72	78	71	77	76
hypind + perhigh	74	70	73	69	81	73
perhigh + persharp	52	59	65	74	100	70
perhigh + perround	55	55	69	72	100	70
perhigh + perblunt	41	64	54	59	63	56
persharp + perround	56	55	69	70	96	69
persharp + perblunt	56	55	69	70	96	69
perround + perblunt	56	58	69	70	96	70
Mean	61	63	69	70	89	70
Three-variable						
hypind + persharp + perround	80	72	84	73	96	81
hypind + persharp + perblunt	80	72	84	73	96	81
hypind + perround + perblunt	80	72	84	73	96	81
perhigh + hypind + persharp	76	70	80	71	100	79
perhigh + hypind + perround	76	70	80	69	96	78
perhigh + hypind + perblunt	76	72	73	69	81	74
perhigh + persharp + perround	52	58	69	74	100	71
perhigh + persharp + perblunt	52	58	69	74	100	71
perhigh + perround + perblunt	52	58	69	74	100	71
Mean	72	68	78	72	96	77
Four-variable						
hypind + perhigh + persharp + perblunt	76	72	80	73	96	79
hypind + perhigh + persharp + perround	76	72	80	73	96	79
hypind + perhigh + perround + perblunt	76	72	80	73	96	79
Mean	76	72	80	73	96	79
Grand mean	67	66	72	70	91	73

[a] Both conservative and radical.

The crown height decreased from 13.0 to 8.0 mm in the bushbuck and we found 75% and 80% sharp cusps. High and rounded morphology was found in four plains reedbucks from horn stages 1–4 with 100% high and rounded cusps. In three African buffaloes, horn stages 1–3, the crown height decreased from 22.9 to 12.8 mm and the cusps were all high and rounded (table 2). Similarly, consistent cusp shape morphology during wear was commonly encountered during the recording of the large data set used in this study.

Cluster Analysis

Cluster analysis, using the index of hypsodonty and all mesowear variables except

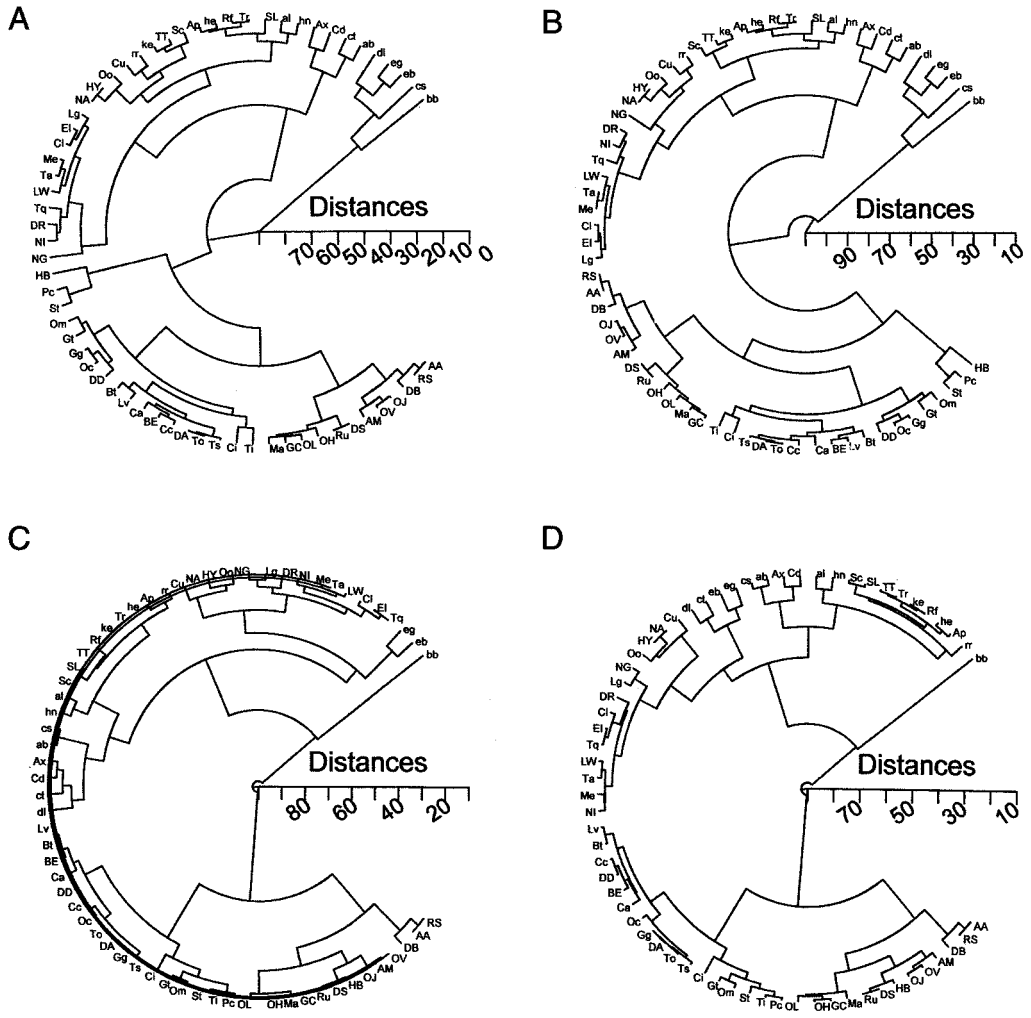

Fig. 2. Hierarchical cluster diagrams of all Recent species included in this study. **A**. Cluster based on index of hypsodonty, percent high occlusal relief, percent sharp cusps and percent blunt cusps. **B**. Cluster based on the same variables as (A) except index of hypsodonty. **C**. Cluster based on percent sharp cusps and percent blunt cusps only. **D**. Cluster based on the same variables as (C) plus index of hypsodonty. Symbols as in table 1. UPPER CASE = BROWSER, lower case = grazer, Mixed Case = Mixed Feeder.

percent rounded cusps, polarizes the full set of 64 Recent species into a pattern that groups grazers and browsers at the extremes, with mixed feeders in between (fig. 2). The figure shows hierarchical cluster diagrams of all Recent species included in this study. *A* is a cluster based on index of hypsodonty, percent high occlusal relief, percent sharp cusps and percent blunt cusps. *B* is a cluster based on the same variables as (A) except for the index of hypsodonty. *C* is a cluster based on percent sharp cusps and percent blunt cusps only whereas *D* is based on the same variables as (C) plus index of hypsodonty. Figure 1 shows that the grazers group more clearly than browsers, which, although clumped at one end, also intersperse with mixed feeders throughout the mixed feeder range. Mixed feeders also intersperse with browsers. There are two main clusters, corresponding to attrition-dominated and abrasion-dominated wear, respectively. The attri-

tion-dominated cluster is divided into two subclusters, one containing mostly browsers, the other mostly browse-dominated mixed feeders. The abrasion-dominated cluster also shows two subclusters, one containing ''extreme'' grazers (bison bb, white rhino cs, topi dl, and the zebras eb, eg), the other containing the rest of the grazers and the graze-dominated mixed feeders (the abbreviations after the names are the labels used in table 1 and the clusters). This second subcluster is also divided into (1) all the remaining grazers, a few graze-dominated mixed feeders, and one browser (the greater kudu TT) and (2) mainly graze-dominated mixed feeders and a set of small species (mainly duikers and hyraxes) that are abrasion-dominated for reasons not related to grazing, as discussed below. Somewhat unexpectedly, the effect of hypsodonty on this pattern is negligible: virtually the same tree is obtained whether hypsodonty is included (fig. 2A) or excluded (fig. 2B). This is universally observed in other sets analyzed but is not shown further here. It is fortunate for the practical reason that the index of hypsodonty is far more difficult to obtain for a species than are the mesowear variables. The omission of occlusal relief (fig. 2C) has a much more noticeable effect, most evident in the disintegration of the grazing cluster seen in the previous analyses. Adding hypsodonty recaptures some of the structure (fig. 2D), but does not produce the clear cluster of grazers seen in figures 2A, B.

In figure 2A and B, two Indian deer (barasingha Cd, chital Ax), usually regarded as mixed feeders, cluster with the second rank of grazers (hartebeest ab, wildebeest ct), and we suspect that they may be best interpreted as grazers, as indeed they are in our ''radical'' classification in table 1. The mixed feeders associated with the third rank of grazers are also all strongly grass-oriented and in some cases (African buffalo Cs, mountain reedbuck Rf) may be equally well classified as grazers. The main anomaly is the greater kudu TT, a browser that persistently clusters with these graze-oriented mixed feeders and grazers. The reason for this anomaly is essentially a simple calibration problem: the greater kudu shows 100% rounded cusps, like many typical grazers such as the common waterbuck (ke). The fact that the cusps of the greater kudu are considerably less rounded is not picked up by our crude analytical procedure.

Close inspection shows that dispersed browsers are principally small species with significantly rounded cusps: the water chevrotain HY; the duikers DR NA NI NG SL; the hyraxes DD, HB, and two selective, long-necked browsers; the gerenuk LW, and the dibatag EI. The water chevrotain and the duikers are well known to be highly frugivorous, and are thus not typical browsers (Gautier-Hion et al., 1980; Kingdon, 1982a; Lumpkin and Krantz, 1984; Feer, 1989; Nowak, 1991). The rounding of their cusps is probably due to the ''tip crushing wear'' typically associated with frugivory (Janis, 1990). The hyraxes are opportunistic feeders with varied diets including (in *Heterohyrax* and *Dendrohyrax*) a high proportion of insects (Kingdon, 1974). Why the grass dominated mixed feeder *Procavia capensis* Pc shows such strong attrition-dominated wear is unclear, but it seems reasonable to treat the water chevrotain, the duikers and hyraxes as a special case (''mabra,'' for ''minute abraded brachydont'') until more information becomes available or a more adequate dietary classification is devised. There is no good reason to exclude the dibatag and the gerenuk, although we hypothesize that their highly selective feeding results in too little attrition to mask even the small amount of abrasion involved. As with the greater kudu, this may also be a calibration problem involving the degree of rounding of the cusps.

Excluding the water chevrotain, the duikers, and the hyraxes produces a more distinct clustering (fig. 3), again with only minor differences due to inclusion (fig. 3A) or exclusion (fig. 3B) of hypsodonty. The mixing of grazers and grass-dominated mixed feeders reported above is still seen, and the greater kudu TT still clusters with these forms, but the remaining browsers are much less dispersed. The mixed feeders, Indian rhinoceros Ru and springbuck Ma, fall among the browsers and the browser bongo BE falls among the attrition-dominated mixed feeders. The springbuck is a selective mixed feeder (Bigalke, 1978) that could well have a mechanically browserlike diet and wear pattern. The Indian rhinoceros is represented

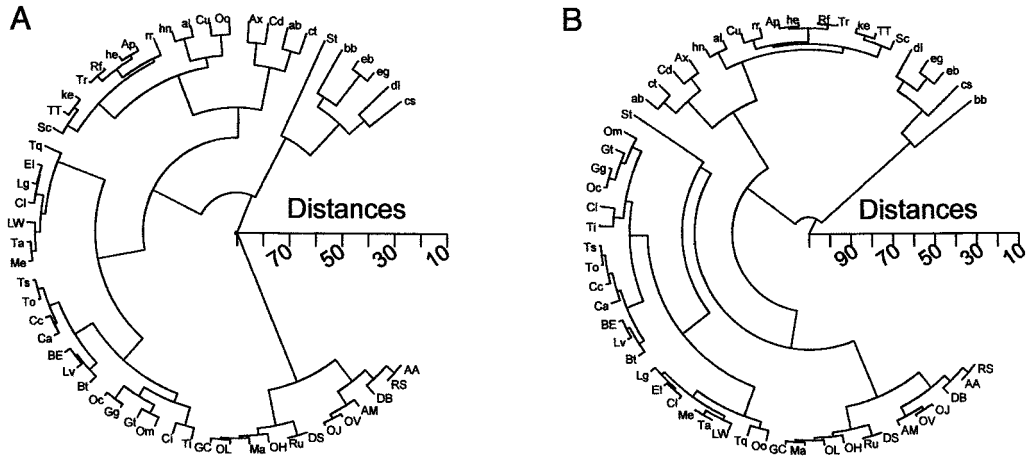

Fig. 3. Hierarchical cluster diagrams of all Recent species included in this study except the ''mabra''—group. **A**. Cluster based on index of hypsodonty, percentage high occlusal relief, percentage sharp cusps, and percentage blunt cusps. **B**. Cluster based on the same variables as (A) except index of hypsodonty. Symbols as in table 1. UPPER CASE = BROWSER, lower case = grazer, Mixed Case = Mixed Feeder.

by a very small sample (5 specimens), and in any case its placement in the less extreme of the two browser clusters is no great anomaly. The bongo is undoubtedly a browser but is said to dig up and ingest roots (Nowak, 1991), a habit that could well account for the extra abrasion detected.

It may be of interest to explore the subset

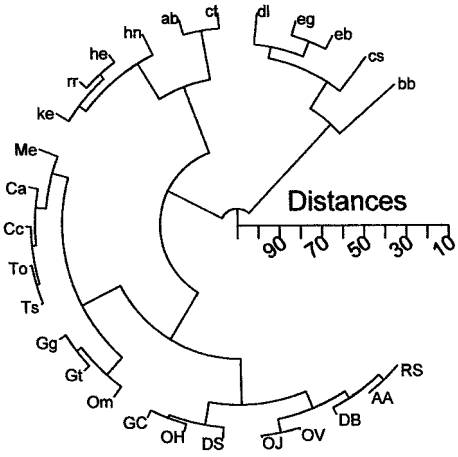

Fig. 4. Hierarchical cluster diagram of a set of ''typical'' Recent species. Cluster based on percentage high occlusal relief, percentage sharp cusps and percentage blunt cusps. Symbols as in table 1. UPPER CASE = BROWSER, lower case = grazer, Mixed Case = Mixed Feeder.

of species for which good dietary data are available and where the interpretation seems to be uncontroversial. We have selected 27 species to form a set of such ''typical'' species. Their clustering pattern is essentially free of anomalies (fig. 4); there are three main clusters, one for true grazers, one for less extreme grazers and mixed feeders, and one for browsers. The grazer-mixed feeder cluster is cleanly divided into two subclusters, one for grazers and one for mixed feeders. The browser cluster is also divided into two, with the slightly more abrasion-dominated Sumatran rhinoceros DS, giraffe GC, and mule deer OH forming their own subcluster. Although such a set of ''typical'' species may not say much about the dietary diversity of living species we feel that it forms a good basis for comparison with fossil forms, as shown below.

The ''typical'' set can also illustrate the relative contribution of individual variables to the resolution of the clusters. For a more comprehensive and quantitative treatment we refer to the discriminant analysis reported below, especially table 3. Figure 5 we show the two most powerful variables and the weakest variable obtained by discriminant analysis for the typical set: percent sharp cusps (fig. 5A), hypsodonty (fig. 5B) and percent high

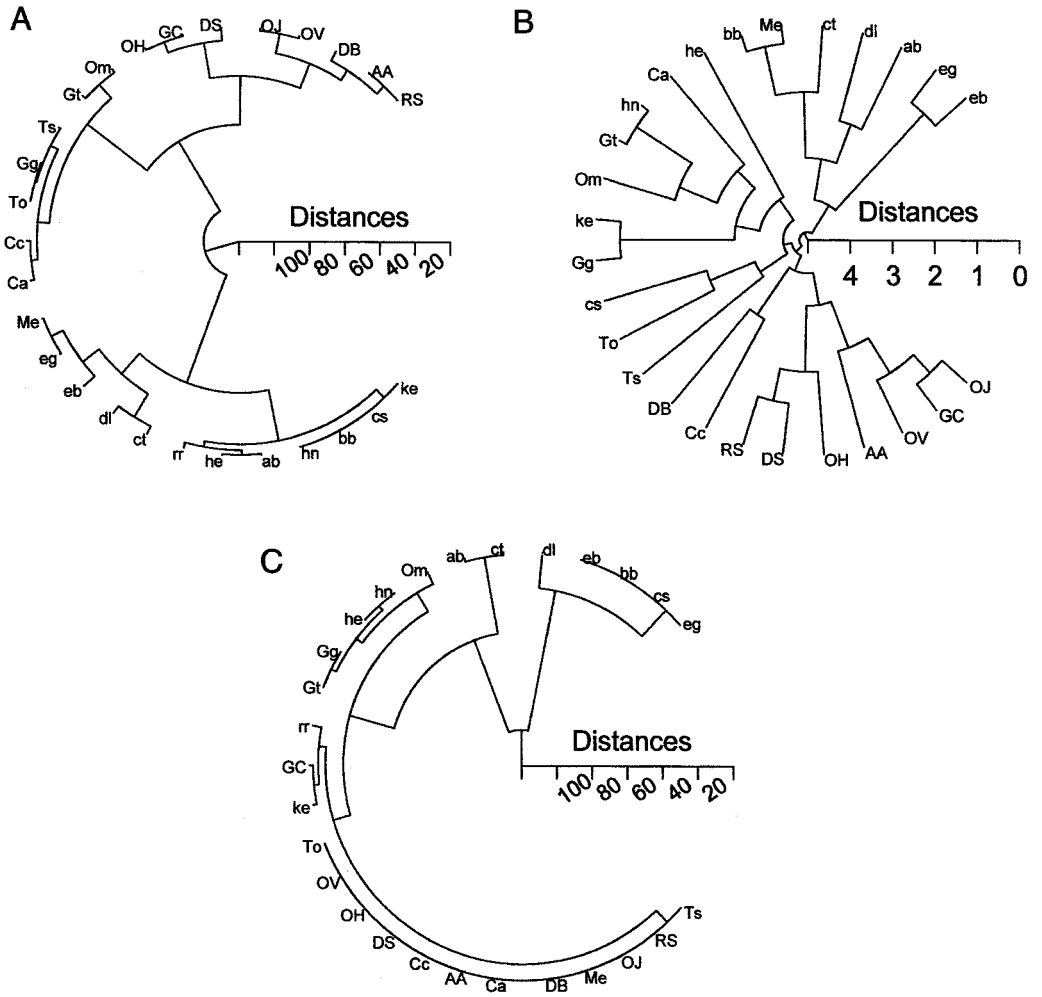

Fig. 5. Hierarchical cluster diagrams of a set of ''typical'' Recent species. **A**. Cluster based on percentage sharp cusps only. **B**. Cluster based on index of hypsodonty only. **C**. Cluster based on percentage high occlusal relief only. Symbols as in table 1. UPPER CASE = BROWSER, lower case = grazer, Mixed Case = Mixed Feeder.

relief (fig. 5C). It is clear that both percent sharp cusps and the index of hypsodonty alone are capable of polarizing the species along a dietary axis, although neither works as well as the full set of mesowear variables. It is also clear that hypsodonty produces a decidedly more mixed result in terms of diet than does percent sharp cusps. The result based on the highly skewed variable percent high relief, is clearly much less satisfactory than the others, but as shown above, it does significantly increase resolution within the dietary classes when used together with the other mesowear variables. Percent high relief seems to be particularly critical for the recognition of grazers and it alone does, in fact, recognize all of the extreme grazers as such (fig. 5C).

Discriminant Analysis

Discriminant analysis was performed to quantify the resolution of mesowear analysis with respect to the three conventional dietary classes of browser, grazer, and mixed feeder. As already shown in the cluster analyses,

mesowear analysis resolves the structure within these classes in a biologically meaningful way, which is completely missed by an analysis based on the main classes only. For example, cusp shape without occlusal relief gives higher scorings but a poorer clustering pattern than does cusp shape with occlusal relief (figs. 2B and C, table 3). These analyses should thus not be seen as a test of ''how well'' mesowear analysis works, only of how well it classifies diet at the most general and conventional level in the different sets of species, and especially of how the ''conservative'' and ''radical'' dietary classifications affect the pattern.

SINGLE-VARIABLE ANALYSES: For the full data set of 64 living species, the single variable that classified the species best was the index of hypsodonty (hypind), with an overall correct classification (jackknifed matrix reported throughout) of 65% for the conservative (cons) and 59% for the radical (radi) classifications (table 3). The second-best single variable was percent high relief (perhigh), which correctly classified 55% (conservative) and 56% (radical) overall. Percent blunt cusps (perblunt) alone correctly classified 58% of radical but only 48% of conservative. The mean of all single-variable analyses of the full set were 50% for conservative and 56% for radical.

For the set without the ''minute abraded brachydonts'' (mabra) the pattern was similar and the percentages correctly classified overall were about 5% higher on average, with hypsodonty index producing 63% for conservative and 57% for radical. Percent sharp cusps (persharp) performed distinctly better for this set, about as well as hypsodonty index, with 61% for conservative and 69% for radical. For the typical set, where conservative and radical coincide, percent sharp cusps (persharp) correctly classified 96% of the species, followed by percent rounded cusps (perround) and hypsodonty index at 81% and a mean single-variable value of 78% (table 3).

TWO-VARIABLE ANALYSES: The combination of hypsodonty index and percent blunt cusps (perblunt) performed best, at 80% correct for conservative and 72% for radical. The index of hypsodonty with persharp also classified well, at 76% for both conservative and radical. Other combinations classified less successfully, with a mean value of 61% for conservative and 63% for radical.

For the minute abraded brachydonts-free set, the pattern was essentially the same but percentages correctly classified averaged 7–8% higher. For the typical set six out of the ten combinations correctly classified 96% or more of the species, percent high relief with either persharp or perround both giving 100% correct.

THREE-VARIABLE ANALYSES: As the number of variables increase the percentage of species correctly classified mounts and the difference between the conservative and radical classifications is reversed, so that whereas the radical classification gets the highest percentages of species correctly classified for one and two variables, from three variables onward, the conservative classification gets the highest scores. For three variables and the full set of species, the combinations of hypsodonty index with any two cusp shape variables performs best (80% correct for conservative, 72% for radical), followed by combinations of hypsodonty index, percent high relief, and any cusp shape variable (76% for conservative, 70–72% for radical). The mesowear variables without hypsodonty give significantly lower values and the pattern is reversed, with higher percentages correctly classified for the radical classification. The mean percentage correctly classified are 72% for conservative and 68% for radical.

For the minute abraded brachydonts-free group, the pattern is the same but the percentages average 6% higher for conservative and 4% higher for radical. For the typical set, all combinations except one correctly classify 96% or more of the species. The exception is hypsodonty index, percent high relief, and percent blunt, at 81% correct. This is a recurring pattern: percent high relief and percent blunt together seem to perform relatively poorly in most combinations of two or three variables. Both variables are highly skewed since most taxa have high relief and few blunt cusps.

FOUR-VARIABLE ANALYSES: All combinations of hypsodonty with occlusal relief and two of the three cusp shape variables give the same result. For the full set of species, 76% (conservative) or 72% (radical) are cor-

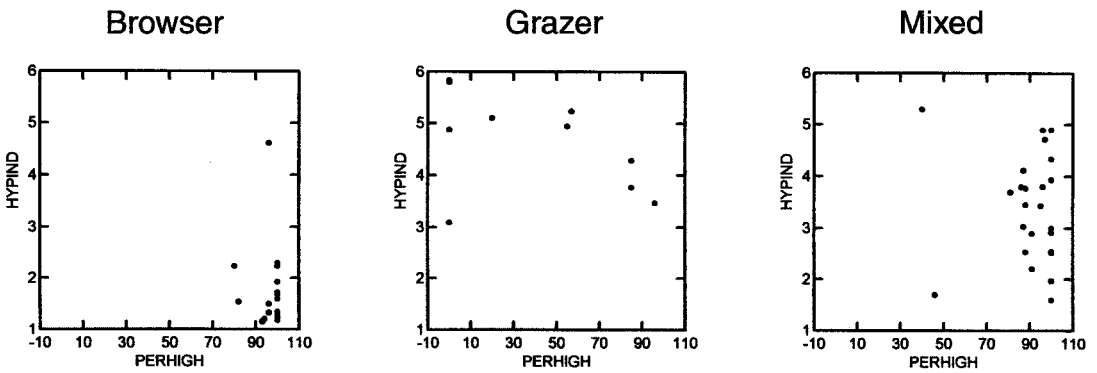

Fig. 6. Bivariate plots for the three dietary classes (conservative classification) of percentage high occlusal relief (PERHIGH) against the index of hypsodonty (HYPIND). Data from table 1.

rectly classified. For the minute abraded brachydonts-free set these values are 80% (conservative) and 73% (radical). The typical set is classified at 96% correct.

Mesowear and Diet—A Closer Look

This section gives a more detailed breakdown of the general patterns found in cluster and discriminant analyses of hypsodonty, occlusal relief, and cusp shape in relation to diet.

Hypsodonty: The index of hypsodonty is significantly different among conservative and radical dietary classes (Kruskal-Wallis test, $P < 0.001$) except that the difference between mixed feeders and grazers is only significant for the conservative classification ($P = 0.003$).

Occlusal Relief: High occlusal relief is the common state except in grazers, which cover the full range (fig. 6). No browser has less than 80% high relief, and only two mixed feeders (the brachydont lesser kudu and the hypsodont saiga) have lower values. The only hypsodont browser, the pronghorn, has 100% high relief, but very high values are also found for most hypsodont mixed feeders. There is no evidence that occlusal relief would systematically change with hypsodonty in browsers or mixed feeders, but in grazers the most hypsodont forms have low relief. These are the ''extreme grazers'' identified by the cluster analyses, primarily the species of *Equus* and certain Alcelaphini. Grazers as a group have significantly lower relief than either browsers or mixed feeders (Kruskal-Wallis test, $P < 0.001$ for both the conservative and the radical classifications). The only species that show predominantly low relief are those of the zebras and the white rhinoceros, which are all plagiolophodont grazers. However, plagiolophodont forms may also show high relief (for example the hipparions included in this study), and feral horses that have lived on browse also show high occlusal relief (unpublished data). Therefore, low relief appears to be a strongly associated with grazing (or at least with highly abrasive food).

Cusp Shape: Cusp shape appears to be largely independent of hypsodonty, as all three cusp shapes occur in all crown height classes (fig. 7). Looking separately at the percentages of sharp, rounded, and blunt cusps allows two further distinctions: no extant grazer has more than 40% sharp cusps, and no browser or mixed feeder has more than 10% blunt cusps. Despite nearly complete overlap of ranges, all three dietary groups in all combinations are significantly different from each other in cusp shape (persharp and perblunt; Kruskal-Wallis test; $P \leq 0.001$ for both conservative and radical), except that mixed feeders are not significantly different from browsers. In most cases cusp shape does not seem to change with hypsodonty, but the only hypsodont browser (the pronghorn) has a very high percentage of sharp cusps, indicating a high attrition level and arguing against any role for abrasive food or dust. In contrast, percent rounded cusps seems to decrease with increasing hyp-

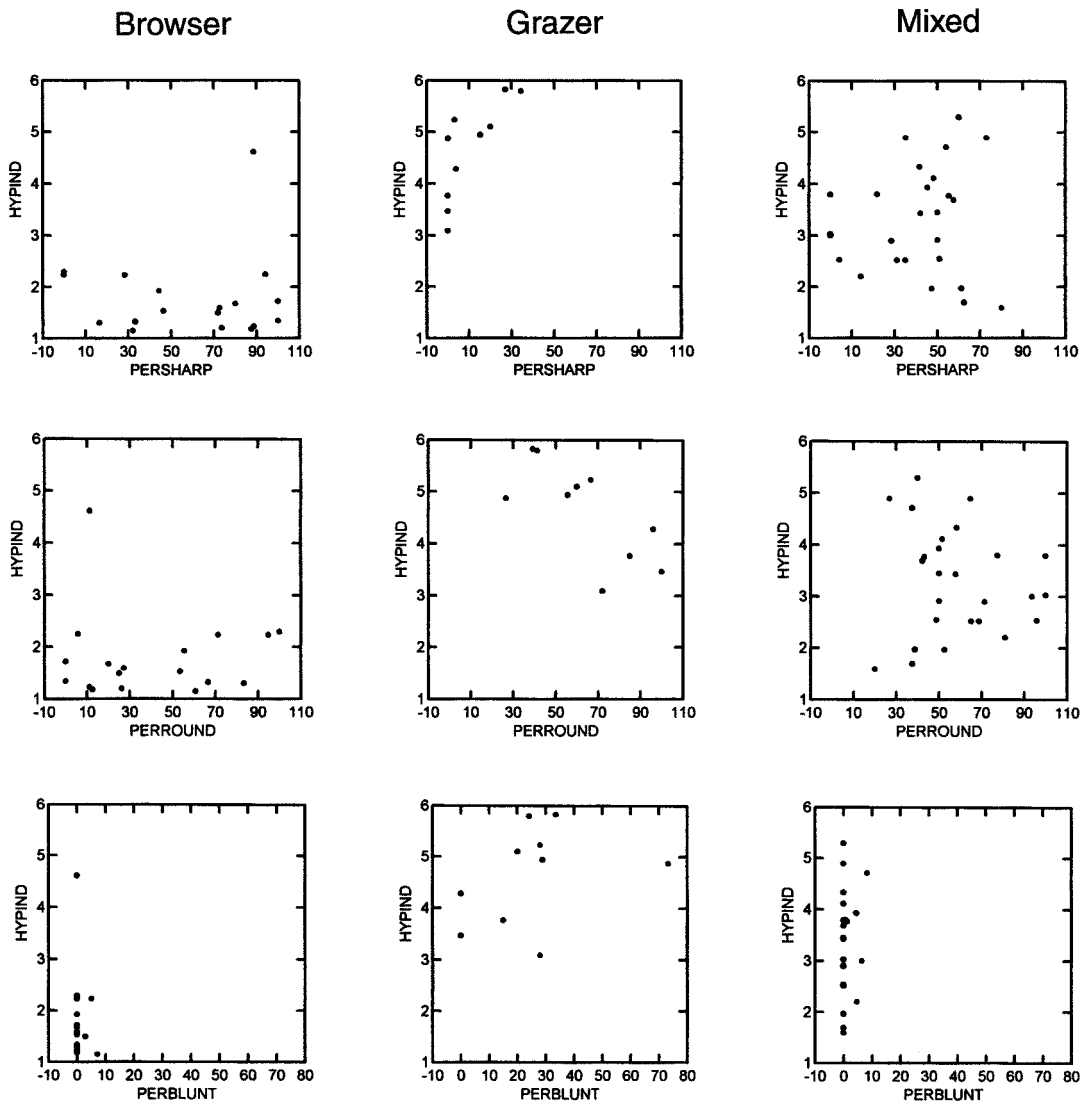

Fig. 7. Bivariate plots for the three dietary classes (conservative classification) of cusp shape. PERSHARP; PERROUND; PERBLUNT) against the index of hypsodonty (HYPIND). Data from table 1.

sodonty in grazers, suggesting that increased abrasion may not be the main reason for the increased wear in these forms. The plots shown in figures 6 and 7 change only in details if the radical dietary classification is used. Hierarchical cluster diagrams for fossil and Recent species are shown in figure 8.

FIGURES OF SELECTED TEETH: A sample of sharp and high relief teeth is shown in figures 9 and 10. Both perissodactyl and artiodaclyl teeth show that the apices are similarly sharp although the relief is clearly higher in artiodactyls. Dots next to each tooth are 5 mm apart; all views are buccal of adult upper molar teeth (mostly M2). Figures 11–15 show teeth of high relief and rounded apices. Again the perissodactyl overall has the lower relief (fig. 15I). We find that the condition of sharp and rounded remain the same despite the degree of relief. For example, figure 14D and 14I have similarly rounded apices but the degree of relief differs. Figure 16 shows high

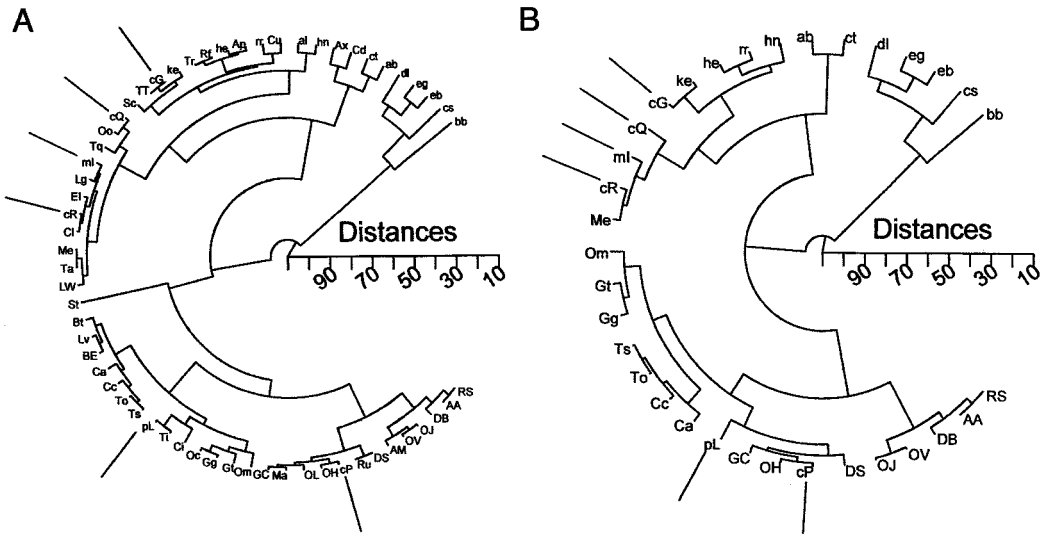

Fig. 8. Hierarchical cluster diagrams, fossil and Recent species. **A**. Fossil species and all Recent species included in this study except the ''mabra''-group. Cluster based on percentage high occlusal relief, percentage sharp cusps and percentage blunt cusps. **B**. Fossil and ''typical'' Recent species. Cluster based on the same variables as (A). Symbols as in table 1. UPPER CASE = BROWSER, lower case = grazer, Mixed case (capital first) = Mixed feeder, mixed case (lower-case first) = fossil Species.

and low cusps which are all rounded whereas figure 17 shows high rounded (17H, K) and low blunt cusps (17F, I). Figures 18 and 19 show low and blunt cusps of perissodactyls. In some of the *Equus* individuals cusp are more than blunt they are convex (fig. 18F and 19D). So far we have classified such convex cusps as blunt. Figures 20 and 21 show cusps of mixed modality. For example, figure 20A shows sharp and rounded cusps on the same tooth. Figure 20I shows a blunt cusp and a rounded cusp on the same tooth. Figure 21A shows strongly blunt cusps and 21D and F mixed rounded and sharp cusps. We find that the mixed patterns within the same dentition are not common.

COMPARISON OF CUSP-SHAPE HISTOGRAMS: The cusp mesowear histograms for a selection of extant species from table 1 are given in figures 22–26. Histograms are based on the raw data and are the same with the summary values given in table 1.

Figure 22 shows the percentages of cusp tip shapes for selected browsers; the data show a large array of differences between species. *Alces alces* is the only species with 100% high and sharp cusps. The remaining browsers can be arranged according to a decreasing percentage of sharp cusps down to *Tragelaphus strepsiceros*, which has 100% rounded cusps. Note that the hypsodont browser *Antilocapra* has a high proportion of sharp cusps, as expected from its diet. *Hyaemoschus* and most duikers (*Cephalophus*) have a small percentage of blunt cusps, probably because of ''tip-crushing'' wear due to frugivory as noted above. *Litocranius* also shows strong rounding, possibly because of the very low overall rate of wear (attrition not enough to mask even very low abrasion). *Dendrohyrax dorsalis* is the only browser in our data set that features some blunt cusps, but as discussed above hyraxes are too omnivorous to be qualified as typical browsers and their dental wear is not well understood.

Figure 23 shows the percentages of cusp tip shapes for selected hypsodont mixed feeders. *Ovibos*, *Saiga*, and *Capra* are attrition-dominated and all species show at least 25% sharp cusps. Blunt cusps are only seen in *Lama* and *Capra*, less than 10% in both cases.

Figure 24 shows the percentages of cusp tip shapes for selected ''traditional'' mixed feeders, arranged from the attrition-dominated *Antidorcas* to the abrasion-dominated *Ae-*

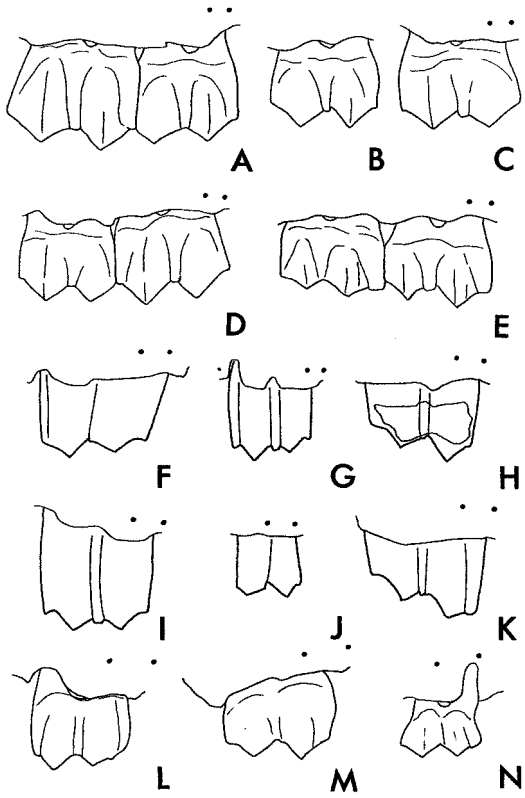

Fig. 9. Relief high, sharp cusps. **A**: *Alces alces* AMNH 6408, left M2-M3; **B**: 207705, left M1; **C**: 19799, right M2; **D**: 98162, right M2-M3; **E**: 173563, left M1-M2; **F**: *Capra ibex* AMNH 82264, left M3; **G**: 11571, left M2; **H**: 69428, right M3; **I**: 117575, left M2; **J**: 69428, right M1; **K**: 57318, right M3; **L**: *Litocranius walleri* AMNH 179215 left M3; **M**: 161173 right M3; **N**: 179217 right M1.

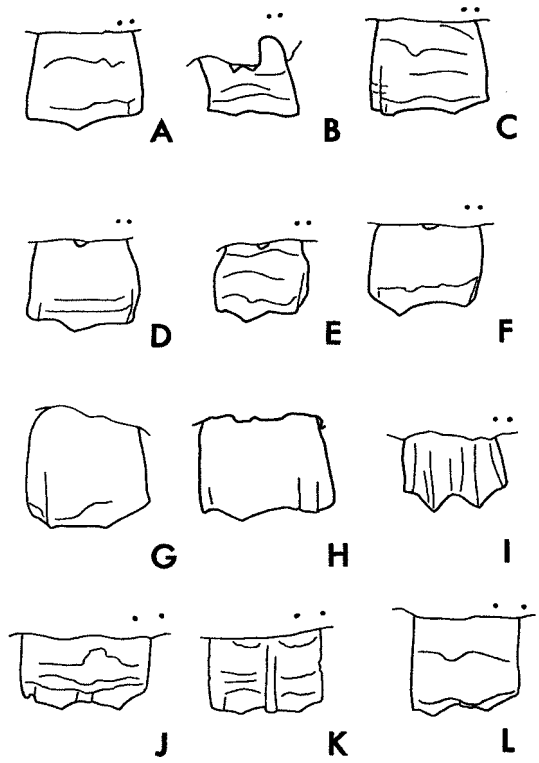

Fig. 10. Relief low and high, sharp cusps. **A**: *Diceros bicornis* AMNH 139694, left M2; **B**: 139692, right M1; **C**: 113776, left M2; **D**: 167693, right M2; **E**: TE 7990, left M2; **F**: AMNH 13778, left M2; **G**: 13776, left M2; **H**: TE 7987, right M2; **I**: *Cervus canadensis* AMNH 40005, left M1; **J**: *Equus burchelli* AMNH 119669, left M2; **K**: 82312, left M2; **L**: 204106, right M2.

pyceros. Most species have about 50% sharp and 50% rounded cusps, while blunt cusps are absent except for a few in *Gazella thomsoni*, the more grass-oriented of the two gazelles.

Figure 25 shows the percentages of cusp tip shapes for some mixed feeders of the Indian monsoon forest. All are highly abrasion-dominated, like African fresh grass grazers (and the browsing greater kudu). The cervids (*Axis axis* and *Cervus duvauceli*) particularly show a grazerlike profile with over 20% blunt cusps, and both are indeed treated as grazers in our ''radical'' dietary classification (table 1).

Figure 26 shows the percentages of cusp tip shapes for grazers. The data show a diversity that promises potential for future palaeodiet analysis. The Reduncini (*Redunca* and *Kobus*) have a very high percentage of rounded cusps, a signal apparently related to marginal or ''fresh grass'' grazing. All other grazers have a significant proportion of blunt cusps. The Alcelaphini (*Connochaetes, Alcelaphus,* and *Damaliscus*) are dominated by rounded cusps but also show significant proportions of sharp and blunt cusps. The zebras (*Equus*) stand out with almost subequal amounts of cusps of each type, while the white rhinoceros (*Ceratotherium*) has over 30% blunt cusps and no sharp ones at all. *Bison* is unique in our data set in having mostly blunt cusps (over 70%).

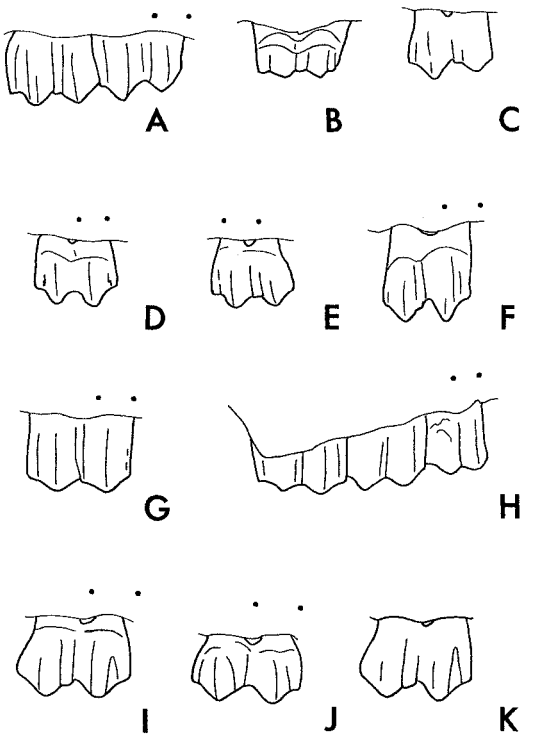

Fig. 11. Relief high, rounded cusps. **A**: *Cephalophus nigrifrons* AMNH 52936, left M2-M3; **B**: 52930, left M3; **C**: 52933, left M2; **D**: 119814, left M2; **E**: 55389, left M2; **F**: *Tragelaphus scriptus* AMNH 36403, right M3; **G**: 163033, left M2; **H**: *Gazella thomsoni* AMNH 163065, right M1-M3; **I**: *Litocranius walleri* AMNH 161173, right M2; **J**: 179215, left M2; **K**: 161174 right M2.

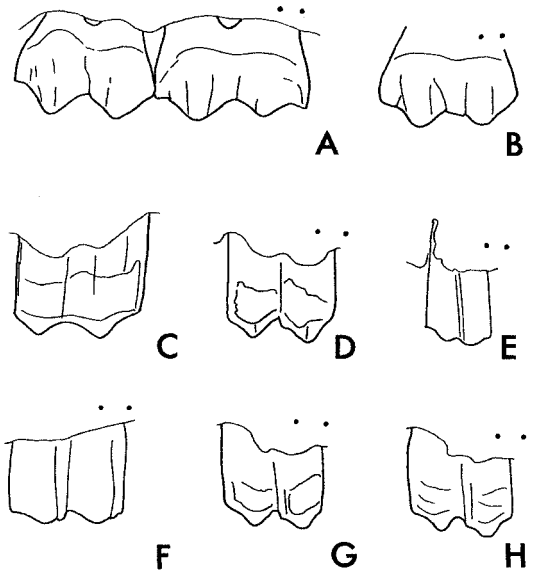

Fig. 12. Relief high, rounded cusps. **A**: *Giraffa camelopardalis* NMNH 251800, left M1-M2; **B**: AMNH 24292, left M2; **C**: *Ovis canadensis* NMNH 16935, right M2; **D**: *Capra ibex* AMNH 82267, left M2; **E**: 11575, left M1; **F**: 57318, M2; **G**: 82264, left M2; **H**: 82207, left M2.

The Serengeti Feeding Succession (Test Case)

Subjective inspection of the mesowear of the five species involved indicates four grazers (*Equus burchelli*, *Alcelaphus buselaphus*, *Connochaetes taurinus*, and *Damaliscus lunatus*) characterized by low relief and numerous blunt cusps, and one browser or browse-dominated mixed feeder (*Gazella thomsoni*) with a higher relief and higher percentage of sharp cusps. Chi square analysis of the cusp shape distribution of all five species in the succession indicates very low probability that the distributions are identical ($P < 0.001$). When the zebra is excluded, the difference is still highly significant ($P < 0.001$), but when only the grazing bovids are compared no significant difference is detected ($P = 0.924$). This is the predicted result because they all feed at the same vegetational level. Comparison of the four grazers also shows a marginally significant difference ($P = 0.025$). *Damaliscus* is represented by only five individuals, however. If it is excluded, the difference between *Alcelaphus*, *Connochaetes*, and *Equus* is more marked ($P = 0.008$). Thus simple analysis of cusp-shape distribution indicates a statistically significant relationship between the species that corresponds to the known one. The same result can also be seen in the cluster diagrams (figs. 2–5; table 4).

Pilot Applications to Fossil Ungulates—table 4

Pachytragus: The samples from the two Quarries at Samos were (marginally) significantly ($P = 0.011$) different in cusp shape distribution although their dentitions are otherwise identical (Gentry, 1971). Neither species showed low relief or blunt cusps, the hallmarks of extreme grazers. Based on microwear analysis, *P. laticeps* has been char-

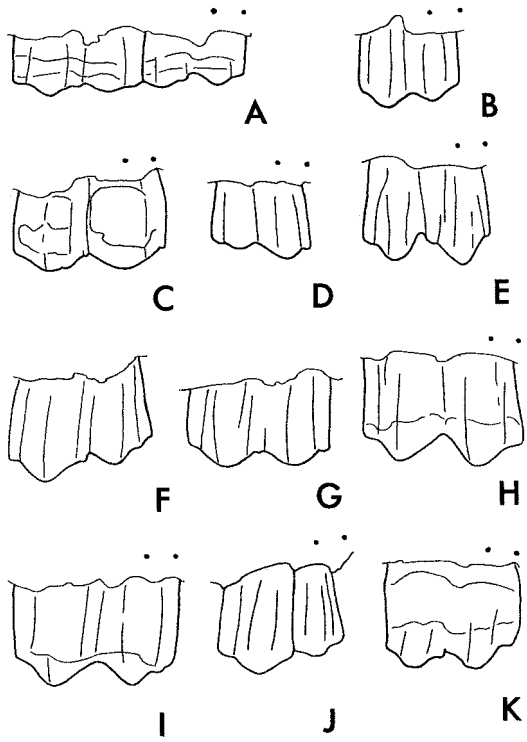

Fig. 13. Relief low and high, rounded cusps. **A**: *Alcelaphus buselaphus* AMNH 114234, right M-M2; **B**: 53432, right M2; **C**: 83516, right M2; **D**: 27677, left M1; **E**: 83513, right M2; **F**: *Connochaetes taurinus* AMNH 81794, right M1; **G**: 216384, right M2; **H**: 31797, right M2; **I**: 31798, left M2; **J**: 81797, right M1; **K**: *Damaliscus lunatus* AMNH 82149, right M2.

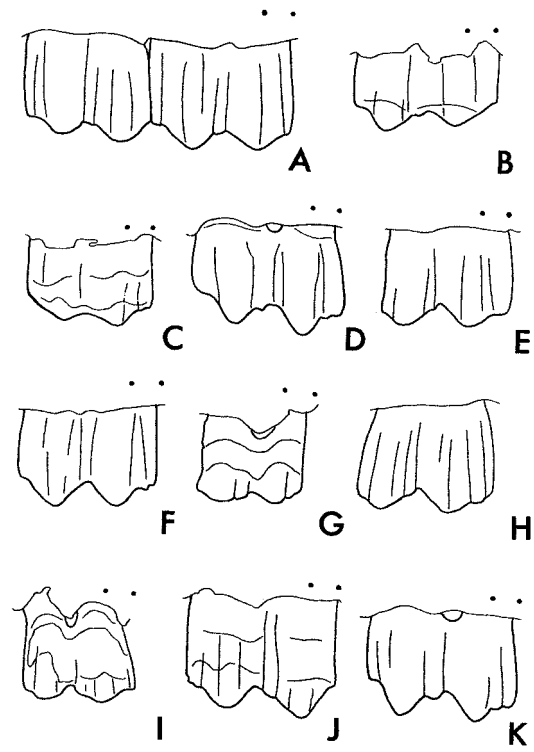

Fig. 14. Relief high, rounded cusps. **A**: *Kobus ellipsiprymnus* AMNH 53484, left M1-M2; **B**: 53476, left M2; **C**: 53479, right M2; **D**: 53496, right M2; **E**: 53455, right M2; **F**: 53496, right M3; **G**: 53479, right M1; **H**: 53496, right M2; **I**: 53496, left M1; **J**: 53496, right M2; **K**: 53497, right M2.

acterized as a grazer and *P. crassicornis* as a mixed feeder (Solounias and Moelleken, 1992b). The mesowear signal suggests the reverse, however; *P. crassicornis* being more abrasion-dominated, with a higher percentage of rounded and a lower percentage of sharp cusps.

In the cluster analysis (fig. 8A), *P. laticeps* is aligned with moderate mixed feeders in the attrition-dominated ''browsing part'' of the tree: the lesser kudu *Tragelaphus imberbis*, *Capra ibex*, *Ovibos moschatus*, and the gazelles. In contrast, *P. crassicornis* falls among more hypsodont and open-adapted mixed feeders in the abrasion-dominated ''grazing half'' of the tree: *Camelus dromedarius*, *Lama glama*, *Aepyceros melampus*, and *Tragelaphus angasi*. In terms of modern analogs, *P. crassicornis* resembles the modern mesodont mixed feeders chousingha (*Tetracerus quadricornis*) and nyala (*Tragelaphus angasi*). *P. laticeps* has mesowear different from all the mesodont species included in the extant data set but appears most similar to mixed feeders such as the gazelles and the lesser kudu.

FOSSIL EQUIDS. The selected four hipparions have microwear data already analyzed by Hayek et al. (1992). As predicted, mesowear clustering (fig. 8A, B) shows *Cormohipparion goorisi* closest to the grazing end of the tree, with the less extreme grazers and grass-dominated mixed feeders, while *Merychippus insignis* and *Cormohipparion quinni* are both placed in the next cluster, with the least extreme of the grass-dominated mixed feeders such as *Tetracerus quadricor-*

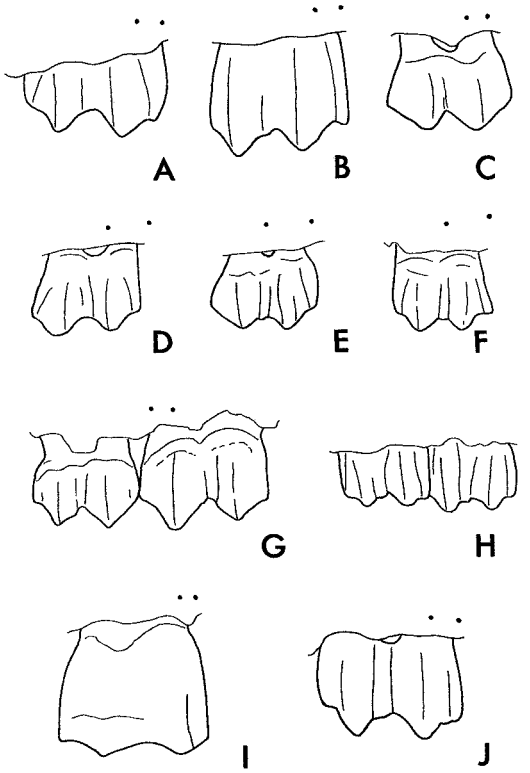

Fig. 15. Relief high, rounded cusps. **A**: *Cervus duvauceli* AMNH 54498, right M2; **B**: 54496, left M2; **C**: Alces alces AMNH 173562, left M1; **D**: *Odocoileus virginianus* ROM 20892, right M2; **E**: 70475, right M2; **F**: 70477, right M2; **G**: *Cervus canadensis* NMNH 100213, left M2; **H**: ROM 25163, right M2-M3; **I**: *Diceros bicornis* TE 7990, right M2; **J**: *Kobus ellipsiprymnus* AMNH 53498, right M2.

nis, *Camelus dromedarius*, and *Lama glama*. *Cremohipparion proboscideum* clusters with the less extreme browsers, near *Odocoileus hemionus* and the mixed feeder *Antidorcas marsupialis*. No hipparions cluster near the zebras.

DISCUSSION

During the six years that we were engaged, on and off, in this study, it became clear that the most commonly raised objection to a mesowear method is that the morphology of occlusal surfaces is too dependent on wear stage to be of use for functional characterization of species. As shown above, this widespread preconception, which we

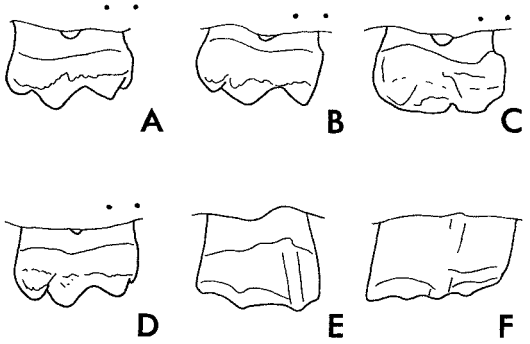

Fig. 16. Relief high and low, rounded cusps. **A**: *Tapirus bairdii* AMNH 8076, left M2; **B**: 80076, left M1; **C**: 35000, left M3; **D**: 35000 left M1; **E**: *Diceros bicornis* TE 7349, right M2; **F**: *Equus burchelli* 34948, left M3.

originally shared, is not valid. The ontogenetic changes that take place in the occlusal configuration are minor, or else restricted to very early and very late wear stages in all the cases that we have been able to study (table 2). We have previously shown that in the African buffalo and several other ungulate species, the wear rate is stable in the adult but slightly higher in the younger individuals and the oldest individuals (Solounias et al., 1994, especially fig.1). We interpret these findings to suggest that wear in ungulates tends to be stable during life, except for the earliest and latest stages, and that this applies to the wear regime recorded by mesowear analysis as well as to the absolute wear rate. Therefore, the scoring procedure for mesowear should not be biased by age composition of the sample if care is taken to exclude the very young and the very old, a precaution easily accomplished.

A related question concerns the robusticity of the patterns themselves. What is the minimum sample size that will bring out the mesowear signature of a species (or more properly a population)? How robust are the results with respect to selection of species and variables?

We have not tried here to address the question of sample size statistically, but extensive practical experience has convinced us that the mesowear pattern stabilizes after about 20 or 30 individuals, and usually gives a reasonable approximation after about 10. This is also the range in which distributions

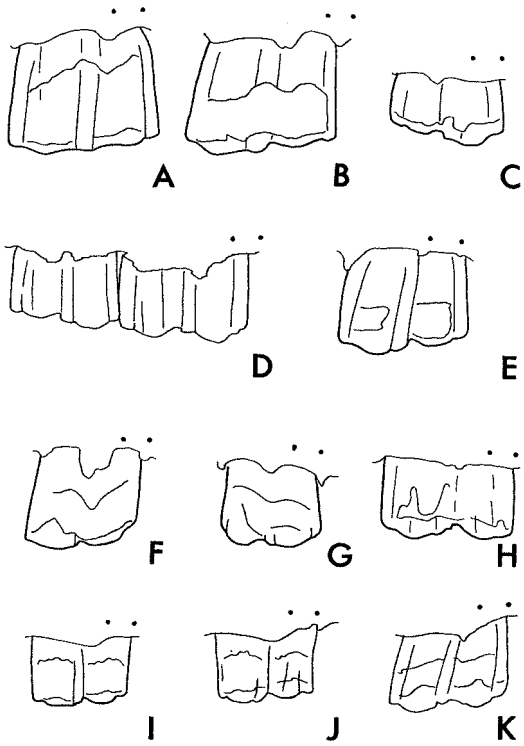

Fig. 17. Relief high and low, rounded and blunt cusps. **A**: *Alcelaphus buselaphus* AMNH 81788, left M1; **B**: 54384, right M1; **C**: 114239, left M1; **D**: 53543, M1-M2; **E**: *Connochaetes taurinus* AMNH 216385, right M1; **F**: 83502, right M1; **G**: 18850, left M1; **H**: 83503, right M2; **I**: *Damaliscus lunatus* AMNH 82144, right M1; **J**: 82144, right M1; **K**: 82150, right M1; High (16B, D, E, H, K) and low blunt cusps (16A, F, I, J). Note that B and E have one high and one low cusp.

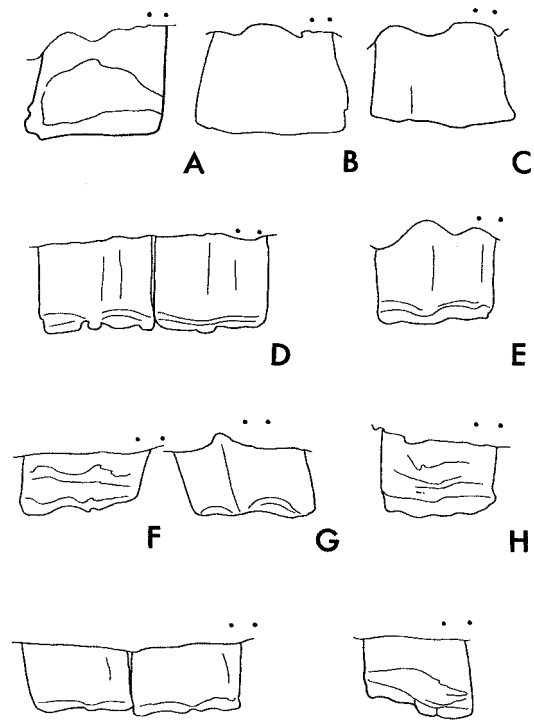

Fig. 18. Relief low, blunt cusps. **A**: *Ceratotherium simum* TE 5919, left M2; **B**: 5926, left M2; **C**: 5923, right M1; **D**: *Equus burchelli* AMNH 82036, right M2-M3; **E**: 82037, left M1; **F**: 119669, left M3; **G**: 54247, right M3; **H**: 119669, left M1; **I**: 165065, right M1-M2; **J**: 16062, left M1.

that look different become significantly different statistically.

Cluster analysis of the mesowear variables groups the extant species remarkably consistently in different sets of species and using different combinations of variables, so at least for a given set of mesowear summary data, the method may be regarded as robust as well as relatively precise: unlike all previously known methods, it appears to resolve details within the main dietary classes. For example, for the mixed feeders microwear provided mostly a bimodal distribution (two clusters); that is, individual specimens were classified either as grazers or browsers (Solounias and Moelleken, 1994), perhaps because microwear studies have been based on small number of specimens (e.g., Solounias and Moelleken, 1992b, 1994; Hayek et al., 1992) and because microwear changes daily (Solounias et al., 1994). The fact that mesowear does recognize not only one but several clusters and subclusters of mixed feeders suggests that, unlike microwear, it averages the browsing and the grazing modes for a particular species to some extent. Therefore it can rank mixed feeders by their relative degree of dental abrasion, which for now is probably justifiably interpreted primarily as proportion of grass in the food.

Discriminant analysis reveals that the resolution of the method increases as additional variables are included, the mean percentage overall correctly classified rising from 53% for one variable to 62% for two variables, 70% for three variables, and 74% for four variables (table 3). As species that appear to

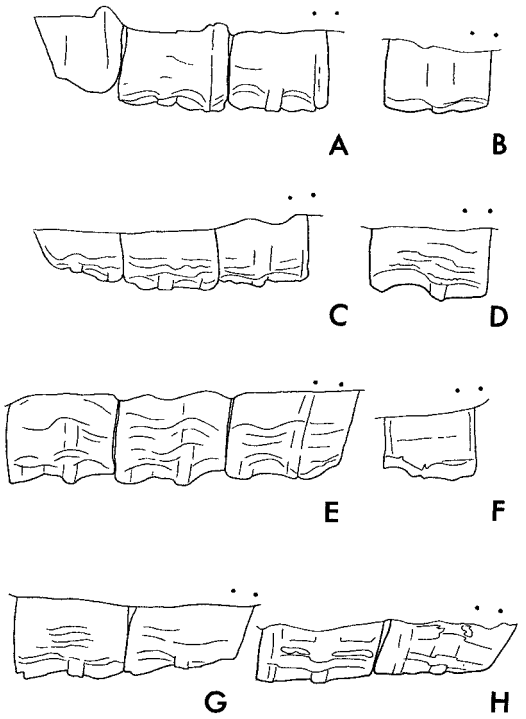

Fig. 19. Relief low, blunt cusps. **A**: *Equus grevyi* AMNH 277427, right M1-M3; **B**: *Equus burchelli* AMNH 83601, left M1; **C**: 27749, right M1-M3; **D**: 165064, left M1; **E**: 82313, left M1-M3; **F**: 182315, right M1; **G**: 82316, left M2-M3; **H**: 82314, left M2-M3.

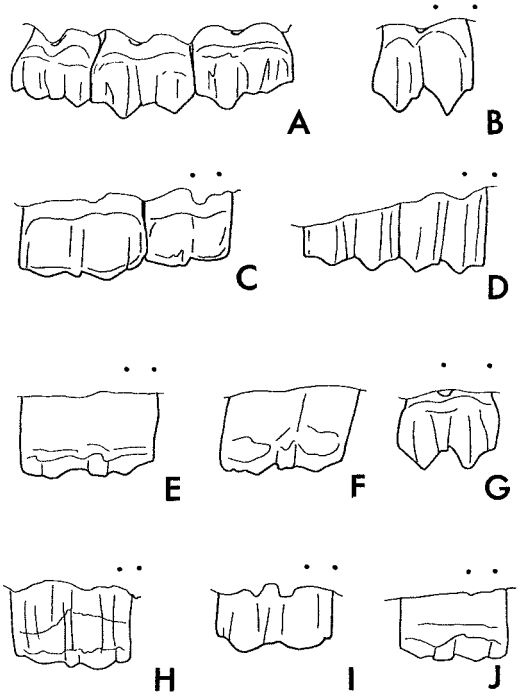

Fig. 20. Relief low, mixed cusps. **A**: *Giraffa camelopardalis* AMNH 83460; **B**: *Tragelaphus scriptus* AMNH 36403, left M2; **C**: *Ovis canadensis* AMNH 35601, right M1-M2; **D**: *Gazella granti* NMNH 82057, right M2-M3; **E**: *Equus burchelli* AMNH 165065, left M2; **F**: 118612, left M3; **G**: *Litocranius walleri* AMNH 179219, right M2; **H**: *Alcelaphus buselaphus* AMNH 54384, right M2; **I**: 11451, right M2; **J**: *Equus burchelli* AMNH 18315, right M2

conform poorly to the simple tripartite dietary classification used or are otherwise problematic are weeded out of the data set, the percentage of correctly classified increases but the pattern remains essentially the same. The best single variable is the index of hypsodonty for both the conservative (65% correct) and the radical (59% correct) dietary classifications, but all single mesowear variables give a better result with the radical classification than with the conservative one. As a result, the mean percentage correctly classified is higher for the radical (56%) than for the conservative (50%) classification. When the number of variables increases this relationship is reversed, so that with four variables the mean is 72% for the radical classification and 76% for the conservative one. For three-variable combinations excluding the index of hypsodonty, the highest percentages correctly classified are much lower, between 50 and 60%, and the pattern is reversed, with the highest values found for the radical classification. The highest percentage correctly classified is consistently given by the index of hypsodonty together with any two-cusp shape variables, 80% for the conservative and 72% for the radical classification.

The index of hypsodonty alone performs slightly better than mesowear without hypsodonty, for both the conservative and the radical classifications, but when combined, hypsodonty and mesowear perform significantly better than either alone. A calibration of the index of hypsodonty by dental structure and shape would probably improve its performance but is quite problematic in practice. Hypsodonty evidently pulls the result

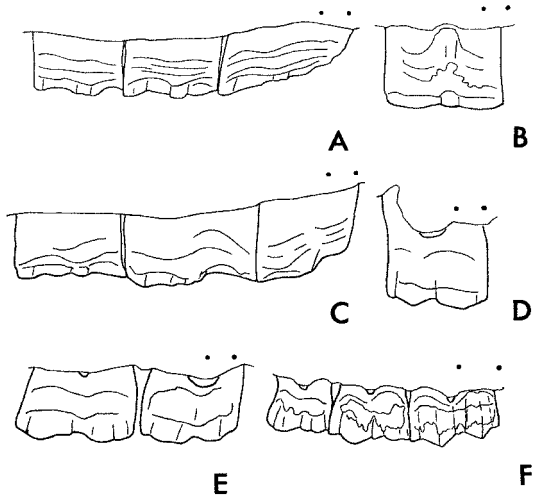

Fig. 21. Relief low or high, blunt cusps and mixed cusps. **A**: *Equus burchelli* AMNH 119672, left M1-M3; **B**: 165063, left M1; **C**: 119635, left M1-M3; **D**: *Kobus ellipsiprymnus* AMNH 53488, left M1M2; **E**: 161707, right M1-M2; **F**: *Cephalophus nigrifrons* AMNH 52938, left M2-M3.

toward the conservative classification, while mesowear moves it toward the radical one. The fact that the mesowear variables produce clusters that appear biologically more distinct than does hypsodonty might indicate that the radical classification is the more natural one. Hypsodonty is essentially a reflection of overall wear rate and its relationship to food properties is expected to be considerably less specific. However, it should be emphasized that the difference between the two dietary classifications is only marginal and that both produce the same main pattern.

The clustering patterns are very robust with respect to the choice of species for analysis. Removing the minute abraded brachydonts, the ''mabra'' group, did not affect the relative placement of the remaining species, and even the species of the small ''typical'' subset retained their relative positions from the more inclusive data sets. The fossil species also fell in homologous clusters between the different data sets. The fact that mesowear analysis does not appear to be overly sensitive to the choice of reference group is reassuring with regard to the practical application of the method. (The choice of reference group is not entirely trivial, however, and is discussed briefly in the Methods (section: Practicalities of Mesowear Data Collection and Analysis.)

Browsers are primarily attrition-dominated, and the blunting that indicates severe abrasion is unknown in this class. Rounded cusps may be common in certain browsers, however, and cause a problem at least under the present scoring procedure in that the slightly rounded cusps of a greater kudu are not distinguished from the strongly rounded cusps of a kob. The problem associated with the the minute abraded brachydont browsers, which for a variety of reasons show strong rounding of cusps, is different; it seems to be at least partly a problem of dietary classification rather than scoring procedure. This is one of several examples highlighting the need for a dietary classification that is closer to the mechanical properties of food materials. For the practical application of the mesowear method to fossil species, the minute abraded brachydont-type problems are not serious, since there is little risk of a small, brachydont form being mistaken for a grazer or grass-dominated mixed feeder. The larger browsers that show rounding of the cusps cause more serious problem. It may be necessary to subdivide the morphological class ''rounded'' into two or more subclasses for better resolution. The unexpectedly large contrast between the giraffe and the moose is food for thought. Could it be that the open habitats of the giraffe are generally dust-infested even at canopy level, so that even a pure leaf diet is abrasive? Certainly the sources of dust are very few in the humid boreal forests, and a general relationship between openness of habitat and abrasion has been proposed before (Janis, 1988). Although we know that there are several factors causing abrasion of teeth, mesowear will not distinguish them, and it might be worth considering methods that combine mesowear and microwear to delve deeper into this interesting problem.

The fact that all ''problem-species'' encountered so far are mesodont or brachydont (and many of them highly so) suggests that mesowear analysis may work better for higher-wear regimes (more hypsodont species). This would hardly be surprising, given the fact that the method is based on the wear

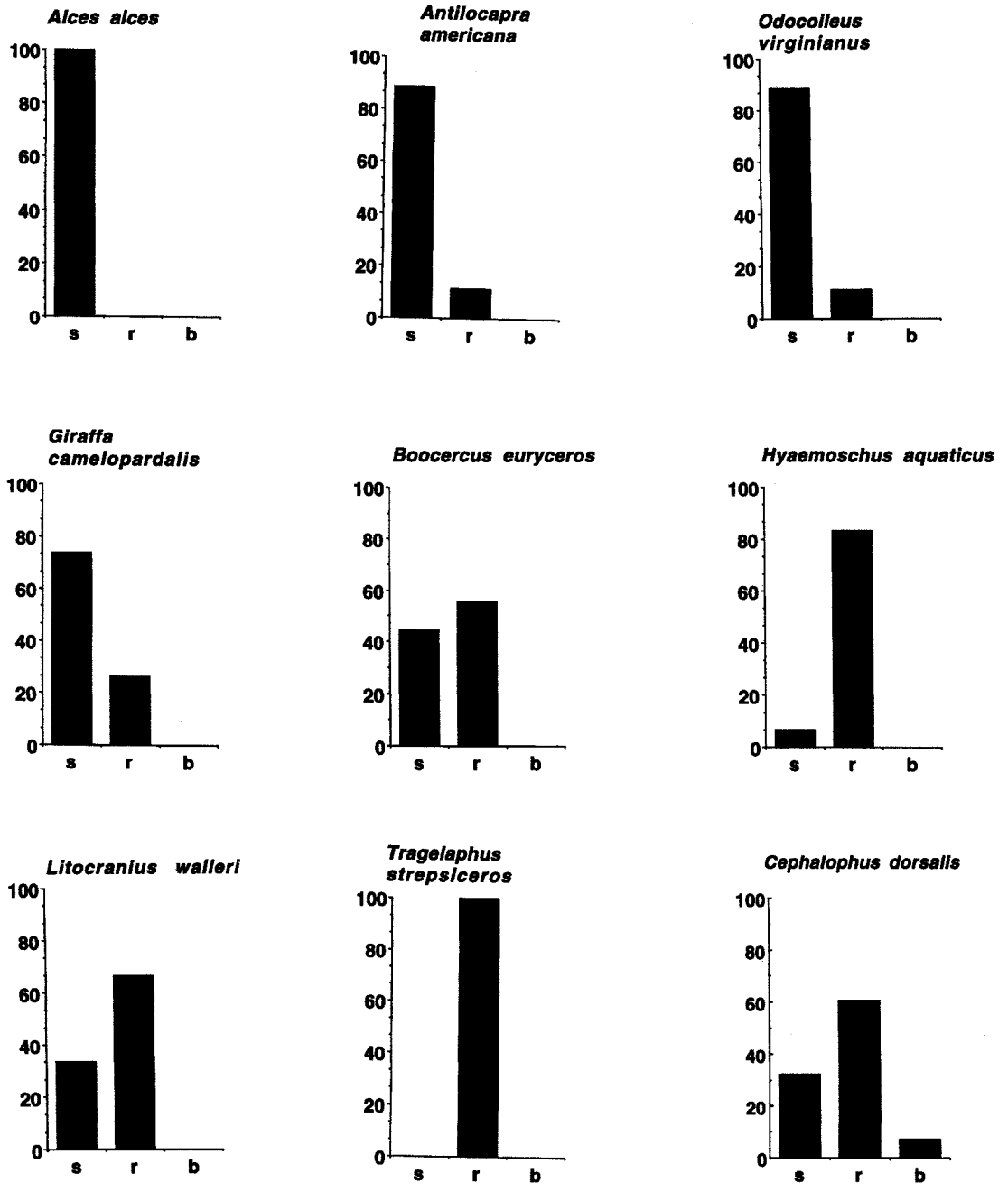

Fig. 22. Selected browsers.

process itself: the more wear overall, the more scope for resolution between abrasion and attrition effects. If this is indeed the case, it is probable that the mesowear signal is inherently biased, so that more hypsodont species appear more polarized in terms of wear and diet than do more brachydont species. This bias, if it exists, is clearly not strong enough to seriously affect analyses like those undertaken here. We are not able to elucidate

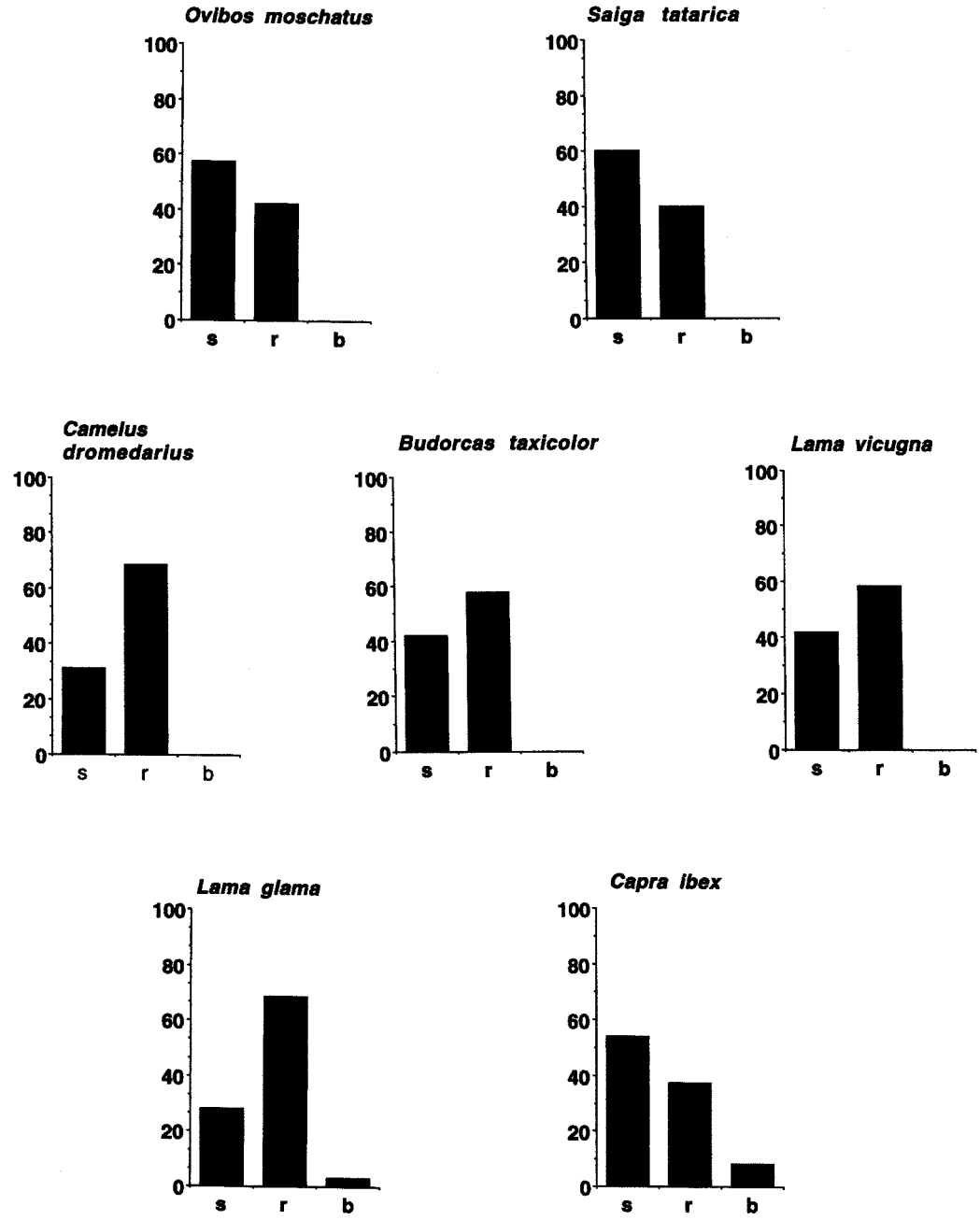

Fig. 23. Hypsodont mixed feeders.

this issue further but the point should be kept in mind in future development of the method. It is especially important to consider this possibility in relation to the many hypsodont, strongly attrition-dominated ungulates found in the Neogene faunas.

Mesowear analysis successfully resolved the ''test case'' of the famous Serengeti grazing succession. Although our samples were drawn from all locations that we were able to include, the result nevertheless replicates the known local sequence, suggesting that at

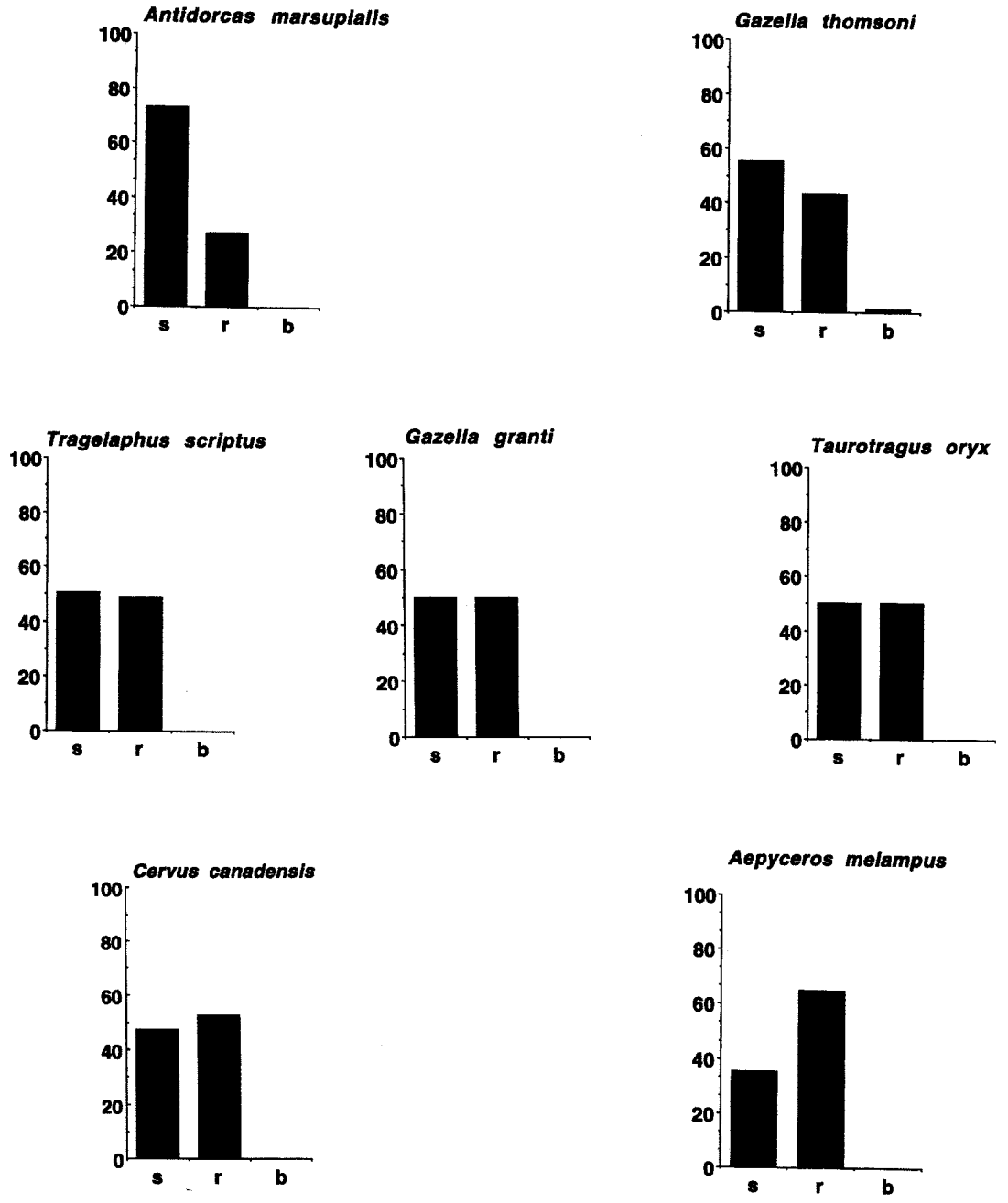

Fig. 24. "Traditional" mixed feeders.

least in this case the interpopulation variation is small enough not to obscure the pattern seen in one particular area.

For the two species of *Pachytragus* the previous microwear results (Solounias and Moelleken, 1992b) and masseter attachment scar analysis (Solounias et al., 1995) were refuted, while Gentry's (1971) original conclusion based on skull shape was supported, by mesowear indicating more abrasion for *P.*

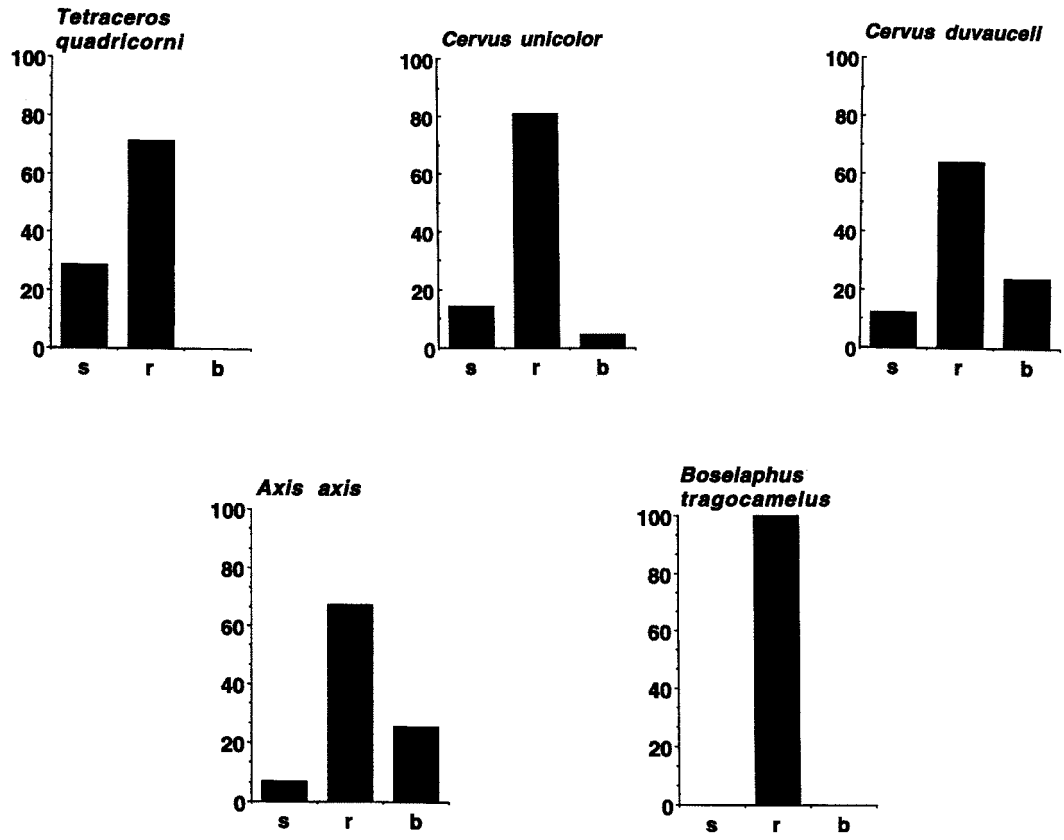

Fig. 25. Indian abrasion-dominated mixed feeders or grazers.

crassicornis than for *P. laticeps*. Closer reading of Solounias et al. (1995) reveals, however, that their conclusion that *P. crassicornis* was further removed from browsing than *P. laticeps* was based on previous microwear analysis, and that the masseter morphology they reported actually suggests the opposite. According to them, *P. crassicornis* ''falls out as a browser for masseteric area, and as a mixed feeder for masseter profundus height, masseter superficialis protrusion, and microwear'' (Solounias et al., 1995: 801). Correspondingly, *P. laticeps* ''falls out as a browser for masseter area and masseter superficialis protrusion, between browsers and mixed feeders for masseter profundus height, and as a grazer for microwear'' (Solounias et al., 1995: 802). Thus mesowear agrees with the conventional wisdom of Gentry (1971) as well as with the muscle scar analysis of Solounias et al. (1995), but disagrees with the microwear analysis of Solounias and Moelleken (1992b). The overall evidence suggests that microwear failed to pick up the averaged, long-term dietary effect detected by mesowear and cranial anatomy analyses.

For the fossil Equidae included in this study, previous microwear analysis identified *Cormohipparion goorisi* and *Merychippus insignis* as mostly grazing while *Cormohipparion quinni* (formerly *C. sphenodus*) and *Cremohipparion proboscideum* were found to be mixed feeders (Hayek et al., 1992: table 4). The 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 probos-*

TABLE 4
Chi Square Analysis of Cusp Shape Distribution in Selected Groups of Species from Three Comparisons

Comparisons: the Serengeti grazing succession, two fossil bovids from the late Miocene of Samos, and three fossil horses from the Miocene of North America. Species labels as in table 1.

Comparison	Chi square	df	P
Serengeti test case			
eb, ab, ct, dl, Gt	78.35	8	0.000
eb, ab, ct, dl	14.426	6	0.025
ab, ct, dl, Gt	64.242	6	0.000
eb, ab, ct	13.929	4	0.008
ab, ct, dl	0.901	4	0.924
ab, ct	0.794	2	0.672
Fossil bovids			
cR, pL	8.147	1	0.004
Fossil bovids vs. Recent ruminants			
cR, Tq, Ta	0.219	2	0.896
pL, Ti, Gt, Gg	13.156	6	0.041
pL, Ti	5.732	1	0.017
cR, Cl	4.627	1	0.031
Fossil equids			
mI, cG, cQ, cP	11.099	6	0.085
mI, cG, cQ	9.512	4	0.049
cG, mI	7.124	2	0.028
cG, cQ	1.255	1	0.263
cG, cP	7.244	1	0.007
Fossil vs. Recent equids			
cG, eb	27.864	2	0.000
cG, cQ, eb, eg	43.885	6	0.000
cG, cQ, mI, cP, eb, eg	54.159	10	0.000
Fossil equids vs. Recent ruminants			
cG, ke, Sc	2.59	2	0.274
cQ, mI, Cl, Lg, Tq	5.339	8	0.721
cP, OH, OL, Ma	11.965	6	0.063

cideum contained only five individuals; some of them did not show the clear browsing signal recorded by mesowear analysis.

Mesowear thus broadly agrees with microwear but appears to offer a stronger signal and more resolution (fig. 8). *Cormohipparion goorisi* is seen to cluster with a set of grazers and abrasion-dominated mixed feeders like the common waterbuck ke and the African buffalo Sc. *Cormohipparion quinni* and *Merychippus insignis* cluster "one step down" with abrasion-dominated mixed feeders such as chousingha Tq, the dromedary Cl and the llama Lg. *M. insignis* also come out as less abrasion-dominated than *C. quinni*. *Cremohipparion proboscideum* clusters far from the other species, with browsers and attrition-dominated mixed feeders like mule deer OH, the roe deer OL, and the springbuck Ma, in a cluster one step removed from that of the pure browsers. This is interesting in view of the old hypothesis that *C. proboscideum* had a proboscis, a feature closely associated with browsing among Recent ungulates (excepting some elephant populations).

The discrepancies revealed between mesowear and conventional microwear analysis should not be underemphasized or taken to suggest that one method is superior to the other. Instead, they are best seen in relation to the different time scales involved. Mesowear shows the long-term, cumulative effect of food, whereas microwear shows a very short-term signal, close to the signal left by the proverbial last supper. Microwear will therefore inevitably be more sensitive to the immediate context of the animal's death than mesowear. Whether this is an advantage or disadvantage depends on the purpose of the analysis, and for a deeper understanding of any given case a combination of both methods seems promising.

The mesowear technique was deliberately designed for the study of broad geographic and temporal trends and contrasts involving the major part of the fossil ungulate community. The fact that it appears to work better than methods demanding many times the amount of work per species investigated came as a pleasant surprise to us, and suggests that more sophisticated mesowear techniques may offer significantly higher resolution in the future. For example, to collect the microwear data of 40 gazelles with the electron microscope took a month while mesowear data for the same sample were collected in 30 minutes. The chief limitation that we envision derives from the trade-off between precision and generality: owing to the influence of dental structure, high-resolution comparisons will probably be difficult to apply between groups with structurally different teeth.

CONCLUSIONS

Together with hypsodonty, the mesowear signature of a species is a robust character-

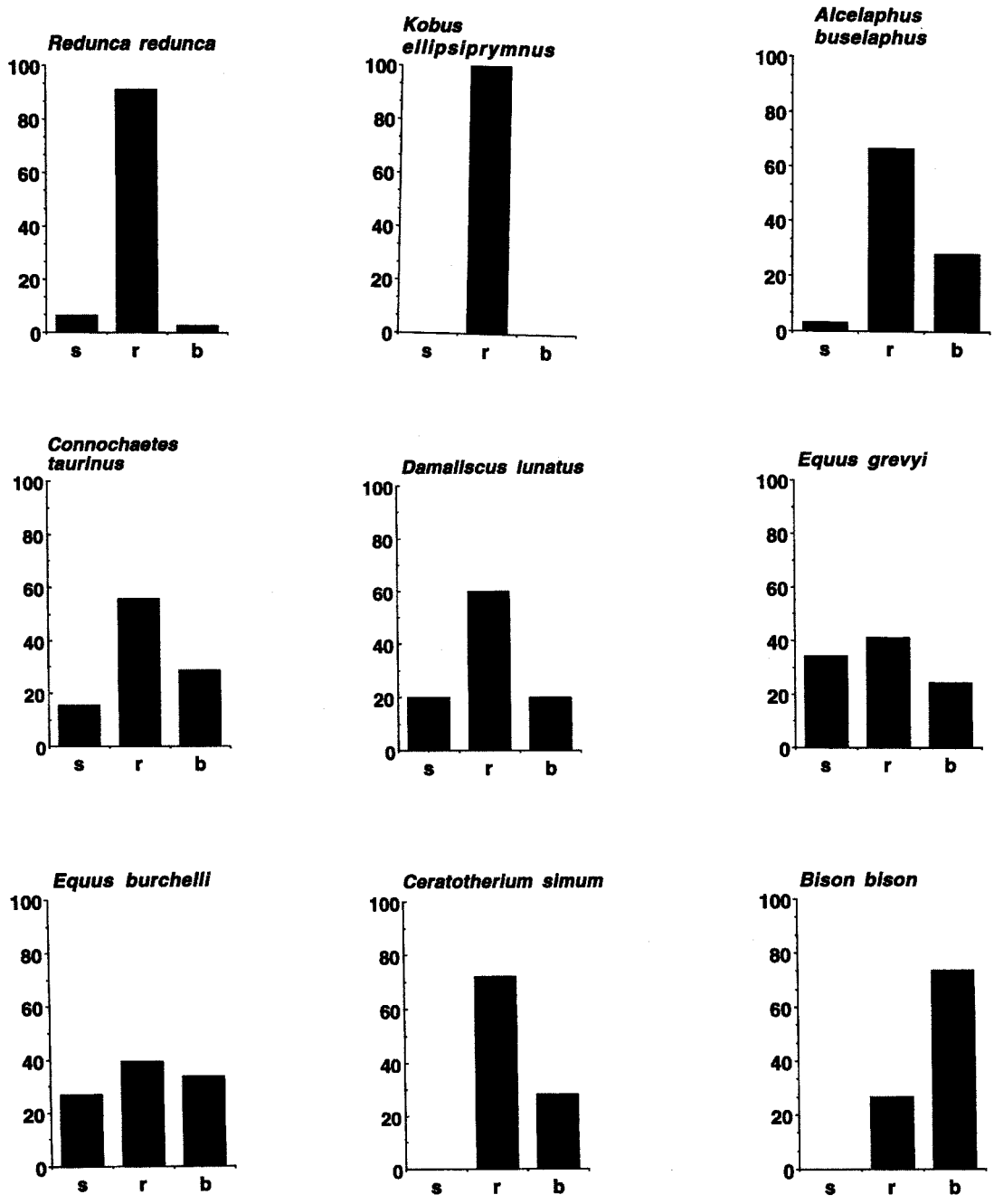

Fig. 26. Grazers.

ization of the mechanical properties of the food that it eats, including whatever extraneous contamination the physical environment provides. Mesowear analysis successfully classifies most Recent species into the conventional dietary categories of browser, grazer, and mixed feeder, and offers significant resolution within these categories. We see two uses for mesowear analysis in paleodiet studies: (1) extinct species or popula-

tions can be placed relative to the dietary spectrum of Recent ones, and (2) extinct species or populations can be compared directly with each other in terms of physical food properties. The first use allows us to classify species into dietary categories, or to determine that ''extinct species X had a diet like Recent species A, B and C,'' while the second allows relative statements such as ''extinct species X had a diet that caused less overall wear and relative more abrasion than the diet of extinct species Y.''

The second kind of usage may well prove ultimately more rewarding. We believe that once significant numbers of fossil species from different times and regions have been scored with the mesowear method, it will be possible to relate changes observed in evolving lineages and communities to specific aspects of diets and habitats. This will greatly facilitate the recognition of dietary-environmental contexts without modern analogs, and the dental evolution and dietary paleoecology of ungulates can be studied directly, without the distortion caused by seeing it through the filter of the Recent.

ACKNOWLEDGMENTS

We sincerely thank all museums for access to specimens. American Museum of Natural History (New York), Museum of Comparative Zoology at Harvard, National Museums of Kenya (Nairobi), National Museum of Natural History (Washington D.C.), Natural History Museum (London), and the Royal Museum of Central Africa (Tervuren, Belgium). Wofgang Fuchs who has passed away helped with the AMNH collections. Very special thanks to Christine M. Janis for much patient discussion of diets and the use of her magnificent ungulate diet database and to John Damuth for his critical analysis of the logic of mesowear analysis and paleodiet reconstruction in general. We also thank: Peter J. Andrews, Ray L. Bernor, Alan W. and Anthea Gentry, Linda Gordon, Jeremy J. Hooker, Paula Jenkins, Meave Leakey, Ross MacPhee, Mary C. Maas, Nina Mudida, Guy Musser, Marie Rutzmozer, Gina Semprebon, Richard Tedford, Richard W. Jr. Thorrington, and Alan Walker. We thank Brenda Jones and the editorial staff at the AMNH and Ed Heck for some of the art work and putting together the figures. The research was supported by NSF IBN 9628263 to (NS) and Academy of Finland projects 33558 and 34080 (to MF).

REFERENCES

Bell, R.H.V.
1971. A grazing ecosystem in the Serengeti. Sci. Am. 225: 86–93.

Bigalke, R. C.
1978. Mammals. *In* M. J. A. Werger and A. C. Van Bruggen (eds.), Biogeography and ecology of southern Africa: 981–1048. The Hague: W. Junk.

Bone, J. R.
1964. The age of the horse. Southwest. Vet. 17: 269–272.

Butler, P. M.
1952. The milk-molars of Perissodactyla, with remarks on molar occlusion. Proc. Zool. Soc. London 121 (4): 777–817.
1972. Some functional aspects of molar evolution. Evolution 26 (3): 474–483.

Chapman, J. A., and G. A. Feldhammer
1982. Wild mammals of North America. Baltimore, MD: The Johns Hopkins Univ. Press.

Every, R. G.
1970. Sharpness of teeth in man and other primates. Postilla. 143: 1–29.

Every, R. G., and W. G. Kühne
1971. Bimodal wear of mammalian teeth. *In* D. M. Kermak and K. A. Kermak (eds.), Early mammals: 23–27. London: Academic Press.

Feer, F.
1989. Comparison des regimes alimentaires de *Cephalophus callipygus* et *Cephalophus dorsalis*, Bovides sympatriques de la foret sempervirente africaine. Mammalia 53: 563–604.

Fortelius, M.
1982. Ecological aspects of dental functional morphology in the Plio-Pleistocene rhinoceroses of Europe. *In* B. Kurtén (ed.), Teeth: form, function and evolution: 163–181. New York: Cambridge Univ. Press.

Fortelius, M.
1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. Acta Zool. Fenn. 180: 1–76.

Gauthier-Pilters, H., and A. I. Dagg
1981. The camel. Chicago: Univ. Chicago Press.

Gautier-Hion, A., L. H. Emmons, and G. Dubost
1980. A comparison of the diets of three major groups of primary consumers of Gabon (primates, squirrels, and ruminants). Oecologia 45: 182–199.

Gentry, A. W.
1971. The earliest goats and other antelopes form the Samos *Hipparion* fauna. Bull. Br. Mus. (Nat. Hist), Geol. 20: 231–296.

Guthrie, R. D.
1990. Frozen fauna of the mammoth steppe: the story of Blue Babe. Chicago: Univ. Chicago Press.

Hayek, L-A., R. L. Bernor, N. Solounias, and P. Steigerwald
1992. Preliminary studies of hipparionine horse diet as measured by tooth microwear. *In* A. Forstén, M. Fortelius, L. Werdelin (eds.). Björn Kurtén—A memorial volume. Ann. Zool. Fenn. 28: 187–200.

Hofmann, R. R.
1973. The ruminant stomach. Nairobi: East African Literature Bureau.
1985. Digestive physiology of the deer-their morphophysiological specialization and adaptation. R. Soc. New Zealand, Bull. 22: 393–407.
1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78: 443–457.

Hofmann, R. R., and D.R.M. Stewart
1972. Grazer or browser: a classification based on stomach-structure and feeding habits of East African mammals. Mammalia 36: 227–240.

Hunter, John P., and M. Fortelius
1994. Comparative dental occlusal morphology, facet development, and microwear in two sympatric species of *Listriodon* (Mammalia: Suidae) from the middle Miocene of Western Anatolia (Turkey). J. Vertebr. Paleontol. 14: 105–126.

Janis, C. M.
1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals and the correlation of these factors with dietary preferences. *In* D. E. Russel, J. P. Santorio, and D. Signogneu-Russel (eds.), Teeth revisited: proceedings of the VII international symposium on dental morphology. Muséum national de Histoire Naturelle Memoir sér. C 53: 367–387.
1990. The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. *In* J. Boucot (ed.), Evolutionary paleobiology of behavior and coevolution: 241–260. Amsterdam: Elsevier.

Janis, C., and M. Fortelius
1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biol. Rev. 63: 197–230.

Jarman, P.
1974. The social organization of antelope in relation to their ecology. Behaviour 48: 215–266.

Jernvall, J., J. P. Hunter, and M. Fortelius
1996. Molar tooth diversity, disparity, and ecology in Cenozoic ungulate radiations. Science 274: 1489–1492.

Kingdon, J.
1974. East African mammals. Vol. 1. London: Academic. Press.
1979. East African mammals (large mammals). Vol. 3 P. B. Ibid.
1982a. East African mammals (bovids). Vol. 3 P. C. Ibid.
1982b. East African mammals (bovids). Vol. 3 P. D. Ibid.

Klingel, H.
1965. Notes on tooth development and aging criteria in the plains zebra *Equus quaga bohemi* Matschie. East. Afr. Wildl. J. 3: 127–129.

Labâo-Tello, J., and R. J. Van Gelder
1975. The natural history of the nyala (*Tragelaphus angasi*) (Mammalia Bovidae). Bull. Am. Mus. Nat. Hist. 155: 319–386.

Lucas, P. W.
1979. The dental-dietary adaptations in mammals. Neues Jahrb. Geol. Palaeontol. Monatsh. 8: 486–512.

Lumpkin, S, and K. R. Kranz
1984. *Cephalophus sylvicultor*. Mamm. Species 225: 1–7.

McDonald, J. N.
1981. North American bison. Berkeley: Univ. California Press.

Nowak, R. M.
1991. Walker's mammals of the world, 5th ed. Baltimore, MD: Johns Hopkins Univ. Press.

Nowak, R. M., and J. L. Paradiso
1983. Walker's mammals of the world, 4th ed. Baltimore, MD: Johns Hopkins Univ. Press.

Osborn, J. W., and A.G.S. Lumsden
1978. An alternative to ''thegosis'' and a re-examination of the ways in which mammalian molars work. Neues. Jahrb. Geol. Palaeontol. Abh. 156: 371–392.
Rautenbach, I. L.
1971. Ageing criteria in the springbok, *Antidorcas marsupialis* (Zimmermann, 1780). Ann. Transvaal Mus. 27: 84–133.
Rensberger, J. M.
1973. An occlusion model for mastication and dental wear in herbivorous mammals. J. Vertebr. Paleontol. 47: 515–528.
Rensberger, J. M., A. Forsten, and M. Fortelius
1984. Functional evolution of the cheek tooth pattern and chewing direction in Tertiary horses. Paleobiology 10: 439–452.
Schaller, G.
1967. The deer and the tiger. Chicago: The Univ. Chicago Press.
1977. Mountain monarchs. Ibid.
Schaller, G., Teng Qitao, Pan Wenshi, Qin Zisheng, Hu Jinchu, and Shen Heming
1986. Feeding behavior of Sichuan takin (Budorcas taxicolor). Mammalia 50: 311–322.
Sinclair, A. R. E.
1977. The African buffalo. Chicago: The Univ. Chicago Press.
Slade, L. M., and E. B. Godfrey
1982. Wild horses. *In* J. A. Chapman and G. A. Feldhamer (eds.) Wild Mammals of North America, pp. 1089–1098. Baltimore: The Johns Hopkins Univ. Press.
Solounias, N.
1981. The Turolian fauna from the island of Samos, Greece. Contrib. Vertebr. Evol. 6: 1–232.
Solounias, N., and L-A. C. Hayek
1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. J. Zool. (Lond.) 229: 421–445.
Solounias, N., and S.M.C. Moelleken
1992a. Tooth microwear analysis of *Eotragus sansaniensis* (Mammalia: Ruminantia), one of the oldest known bovids. J. Vertebr. Paleontol. 12: 113–121.
1992b. Dietary adaptation of two goat ancestors and evolutionary considerations. Geobios 6: 797–809.
1994. Dietary differences between two archaic ruminant species from Sansan, France. Hist. Biol. 7: 203–220.
Solounias, N., M. Fortelius, and P. Freeman
1994. Molar wear rates in ruminants: a new approach. Ann. Zool. Fenn. 31: 219–227.
Solounias, N., S. M. C. Moelleken, and J. M. Plavcan
1995. Predicting the diet of extinct bovids using masseteric morphology. J. Vertebr. Paleontol. 15: 795–805.
Sondaar, P.
1971. The Samos *Hipparion*. K. Ned. Akad. Wet. Ser. B 74: 417–441.
Teaford, M. F., and O. J. Oyen
1989. Differences in the rate of molar wear between monkeys raised on different diets. J. Dent. Res. 68: 1513–1518.
Teaford, M. F., and A. Walker
1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. Am. J. Phys. Anthropol. 64: 191–200.
Tener, J. S.
1965. Muskoxen in Canada. Ottawa: Can. Wild. Serv.
Van Valkenburgh, B., M. T. Teaford, and A. Walker
1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabertooth cat, *Smilodon fatalis*. J. Zool. (London) 222: 319–340.
Walker, A. W.
1984. Mechanisms of honing in the male baboon canine. Am. J. Phys. Anthropol. 65: 47–60.
Webb, S. D.
1983. The rise and fall of the late Miocene ungulate fauna in North America. *In*: M. H. Nitecki (ed.), Coevolution: 267–306. Chicago: Univ. Chicago Press.

APPENDIX. Abbreviations

B, browser

b, brachydont

Class, meaning a group in the cluster diagrams and not the term used officially in systematics

cons, conservative dietary classification; doubtful cases are treated as intermediate (mixed feeder)

df, degrees of freedom

fo, fossil

G, grazer

h, hypsodont

hyp, hypsodonty class (b brachydont, h hypsodont, m mesodont)

hypind, index of hypsodonty, from (Janis, 1988)

jad1, dietary classification of Janis (1988) (B unspecialized browser, F fresh grass grazer, H high-level browser, M mixed feeder in open habitat, S selective browser, W mixed feeder in closed habitat)

jad2, jad1 adjusted to tripartite classification of cons and radi. Jad2 gives the corresponding value translated to the simple browser–grazer–mixed feeder classification. Classification differs from that of Janis (1988) for three species: *Antilocapra americana*, *Capreolus capreolus*, and *Procavia capensis*, but agrees with the present opinion of Dr. Janis (personal oral comm. July 1999)

M, mixed feeder

m, mesodont

mb or "mabra", minute abraded brachydont, identified under Results

no, no particular class

P, probability

Percentage Correctly Classified Cases, (jackknifed matrix) in discriminant analysis of groups of species

perhigh, percentage high occlusal relief

persharp, percentage sharp cusps

perround, percentage rounded cusps

perblunt, percent blunt cusps

radi, radical dietary classification; where doubtful cases are treated as extreme (i.e., browser or grazer)

ty, typical of its dietary class

typical, arbitrarily selected set of species with uncontroversial dietary class using different combinations of variables and two dietary classifications

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://nimidi.amnh.org. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).