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Preliminary studies of hipparionine horse diet as measured by tooth microwear

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Hipparionine horses were evolutionarily diverse members of Neogene Holarctic paleofaunas. In this study, we have sampled 13 hipparionine species for a statistical analysis of tooth microwear features used as a basis for dietary interpretation. Our methodology included the generation of two statistical models: first, a two-group model to characterize a suite of browsing and grazing perissodactyls; second, a four-group model to characterize browsing and grazing perissodactyls in combination with browsing and grazing artiodactyls. Fisher's classification functions were used to transform hipparion species from their raw microwear measure space into the spaces defined by each of the two models separately. Our observations on hipparionine dietary modes reveal that they did not exclusively graze, but rather showed a mosaic of dietary preferences.

1. Introduction

Hipparionine horses have been studied for over 150 years. They have been most intensively investigated during the last 10 years, with particular emphases being placed on the group's taxonomy, phylogeny, geochronologic and biogeographic ranges (Woodburne & Bernor 1980, MacFadden 1984, Bernor et al. 1989). In the Old World at least, hipparions were long believed to herald the shift from forest to "savanna-grassland" environments (see Gromova 1952 and Bernor & Hussain 1985 for reviews of this literature), and have been assumed by most workers to have marked a major grazing adaptation (Webb 1983, MacFadden & Hulbert 1989). Recent investigations have revealed that some Old World hipparion taxa lived in warm mesophytic forest environments (Tobien 1986, Bernor et al. 1988), and may have had diets which were not predominantly grass. Indeed, New World (MacFadden 1984, Hulbert & MacFadden, in review) and Old

World (Bernor et al. 1989) hipparions are evolutionarily quite diverse, and evidence has been forwarded that their diversity and adaptation may have coincided with their associated various floral communities (Bernor et al. 1990).

An analysis of hipparionine tooth microwear is of considerable interest since these extinct equid species were such dominant members of Neogene Holarctic paleofaunas (Webb 1983, Bernor et al. 1989). An interesting paleobiological issue is whether hipparion morphological and systematic diversity coincides with specific dietary adaptations. Because of the abundance of hipparion skeletal material, and the laborious procedures involved in collecting and analysing microwear samples, such a study will require mounting a major research effort. Therefore, we provide here a methodology for studying hipparion diet, as well as preliminary results on a small sample of hipparions with comparative extant perissodactyl and artiodactyl material. We hope that this, and subsequent studies, will help to steer a cogent course for investigating the dietary diversity and adaptation of hipparionine horses.

2. Materials

Abbreviations

AMNH: American Museum of Natural History Department of Mammalogy Collections, New York
BMNH: British Museum of Natural History, London
F:AM: Frick Collections, American Museum of Natural History
MCZ: Museum of Comparative Zoology, Cambridge
NMK: National Museums of Kenya, Nairobi
NMNH: National Museum of Natural History, Washington D.C.
PM: Photomicrograph
SEM: Scanning electron microscope

Hipparionine horses

Mi: *Merychippus insignis*
Cog: *Cormohipparion goorisi*
Cos: *Cormohipparion sphenodus*
Coo: *Cormohipparion occidentale*
Hgig: *"Hipparion" giganteum*
Hdie: *Hipparion dietrichi*
Crmed: *Cremohipparion mediterraneum*
Crpro: *Cremohipparion proboscideum*
Crmat: *Cremohipparion matthewi*
Crsp2: *Cremohipparion* sp. 2
Crsp3: *Cremohipparion* sp. 3
Crfor: *Cremohipparion forsteni*
Crlic: *Cremohipparion licenti*

Extant Perissodactyla

Dbic: *Diceros bicornis*
Tter: *Tapirus terrestris*
Tbai: *Tapirus bairdi*
Tind: *Tapirus indicus*
Ebur: *Equus burchelli*

Extant Artiodactyla (Bovidae)

Beur: *Boocerus eurycerus*
Lwal: *Litocranius walleri*
Ggra: *Gazella granti*
Tory: *Taurotragus oryx*
Ctau: *Connochaetes taurinus*
Kell: *Kobus ellipsiprymnus*

The hipparionine adult dentitions we used originated entirely from the F:AM collections. These included 60 specimens belonging to 13 species (Table 1): *Merychippus insignis* (*n* = 11); *Cormohipparion goorisi* (*n* = 9); *Cormohipparion sphenodus* (*n* = 10); *Cormohipparion occidentale* (*n* = 1); *"Hipparion" giganteum* (*n* = 2); *Hipparion dietrichi* (*n* = 13); *Cremohipparion mediterraneum* (*n* = 2); *Cremohipparion proboscideum* (*n* = 5); *Cremohipparion matthewi* (*n* = 1) ; *Cremohipparion* sp. 2 (*n* = 2); *Cremohipparion* sp. 3 (*n* = 2); *Cremohipparion forsteni* (*n* = 1); *Cremohipparion licenti* (*n* = 1). The taxonomic nomenclature follows Bernor et al. (1989).

Extant specimens were obtained from the AMNH, BMNH, MCZ, NMNH and NMK collections. We selected extant perissodactyls, and especially zebras, for comparisons. While acknowledging that distinctions in masticatory function do exist, they are evolutionarily most closely related to hipparions. Moreover, hipparions have generally been thought to have had a dietary regime paralleling *Equus*. We did not use *Equus caballus* because the museum collections available to us did not originate from a region where they lived wild in their natural habitat. Our sample included (Table 2): 74 specimens belonging to five species: *Diceros bicornis* (*n* = 10); *Tapirus terrestris* (*n* = 14); *Tapirus bairdi* (*n* = 19); *Tapirus indicus* (*n* = 2); *Equus burchelli* (*n* = 29).

We also selected a total of 145 bovid artiodactyl specimens, belonging to six species, whose wide range of diets have been well studied (Table 2): *Boocerus eurycerus* (*n* = 15); *Litocranius walleri* (*n* = 24); *Gazella granti* (*n* = 40); *Taurotragus oryx* (*n* = 22); *Connochaetes taurinus* (*n* = 26); *Kobus ellipsiprymnus* (*n* = 18). These species are a subset of a series of species currently being analysed by Solounias and Hayek.

3. Methods

3.1. Preparation of specimens

Methods for preparation and analysis were identical to those which have been used by Solounias et al. (1988). We used only the upper second molar of each specimen. The second crest of the center of the enamel band as measured in the direction of the buccal side was the location for the sampled section. This region was determined to be the most likely to be similar across the selected specimens. Our selection of extant species was made in order to sample various known dietary preferences, and provide a broad spectrum of comparison for interpreting the hipparionine sample (Table 1). We avoided cutting edges on the buccal side and trailing lingual edges to enhance the comparison. Cheek teeth were cleaned with cotton swabs. The cleaning sequence included removal of museum shellac with Zip Strip (Star Bronze Company, Alliance Ohio 44601), washing with detergent and water, washing with bleach, rinsing and drying with 100% ethanol. Zip Strip is an alcohol based jelly-like reagent which has been tested and shown not to affect the enamel of fossil or recent teeth.

A polysiloxane dental impression material ("Express Light Body Regular Set", 3M Dental Products, St. Paul, Minnesota 15144), was used to make high-resolution molds of right M^2 paracone enamel surfaces (whenever possible). Plastic tooth replicas were made with "Epoxydent" dental epoxy die material (Oxy Dental Products, Inc. 6 Hoffman Place, Hillside, New Jersey 07205). To avoid filling defects in the positive casts, the epoxy was driven into the mold using a hand centrifuge.

The replicas were mounted with epoxy glue, silver painted at the base for better conductivity, sputter coated with 200 angstroms of gold, and examined in the secondary mode using an Etec Omniscan SEM. Standardized PMs of 5OOX magnification were taken of representative regions of the enamel band with no tilt.

For each PM (which the microscope manufacturer has set to represent an area of 30,000 square microns), the number of features per field and the length and width of each feature were digitized (using a digitizer, Jandel Scientific Model 2210-0.30 C, 2656 Bridgeway, Sausalito, California 94965) and an IBM XT computer. A software program written by Dr. Earl Weir con-

Table 1. Hipparionine species and sample sizes with paleontologic and morphologic information.

Taxon	Sample size	Age range	Geographic distribution	Facial fossae	Nasal retraction
Merychippus insignis	11	15–6 Ma	N. Amer.	POF	Anterior to P^2
Cormohipparion goorisi	9	15 Ma	N. Amer.	POF, Bucc	Anterior to P^2
C. sphenodus	10	14–12 Ma	N. Amer.	POF, Bucc	Anterior to P^2
C. occidentale	1	12–8 Ma	N. Amer.	POF, Bucc	To anterior P^2
"Hipparion" giganteum	2	ca 8Ma	Greece, USSR	POF, Bucc	To anterior P^2
Hipparion dietrichi	13	8–6 Ma	Greece	vestigial POF, Bucc	To anterior P^2
Cremohipparion mediterraneum	2	8–6 Ma	Greece, China	POF, Bucc, Can	To P^2 mesostyle
C. proboscideum	5	8–6 Ma	Greece	POF, Bucc, Can	To P^3 mesostyle
C. sp. 2	2	8–6 Ma	Greece	POF, Bucc, Can	
C. sp. 3	2	8–6 Ma	Greece	POF, Bucc, Can	
C. forsteni	1	9–7.5 Ma	China	vestigial POF, Can	To P^3 mesostyle
C. licenti	1	5–3 Ma	China	POF, Bucc, Can, Malar	To M^1 mesostyle

verted PM dimensions into microns and recorded the total feature frequency, and the length and width of each feature.

3.2. Basic microwear features and variables

As in previous studies (Teaford & Walker 1984, Teaford 1985, 1986, 1988, Solounias et al. 1988), microscopic features were categorized as either pits or scratches based on their length:width ratio. Gordon (1982) and Grine (1986) have divided enamel features into pits and scratches subjectively based upon orientation angle. For the present work, enamel features with a ratio less than or equal to 4 were categorized as pits, and those with a ratio greater than 4 were categorized as scratches. The 4:1 ratio cut-off point most closely approximates the one used by individuals asked to classify visually enamel wear features into pits and scratches (Grine 1986).

The extant perissodactyls were subdivided into two dietary groups based on their known dietary regimes:

1) the browsers, which have diets resembling in certain ways both those of browsing and intermediate bovid feeders (Tind, Tter, Tbai and Dbic, total $n = 45$), and
2) the grazer, a zebra (Burchell's zebra, $n = 29$).

Extant bovids were subdivided into three groups:

1) browsers (Beur, Lwal $n = 39$),
2) intermediate feeders (Ggra and Tory, n = 62), and
3) grazers (Kell and Ctau, $n = 44$).

Figures 1–3 show some representative photomicrographs of specimens used in this analysis. The grazers have more scratches and less pits, in general, while the reverse is the case for the browsers.

Table 2. Dietary information of the extant species.

Bovid and perissodactyl herbivores and their general diet	Museum	N	Location	General habitat
Browsers, tree and shrub foliage eaters				
Boocerus eurycerus (bongo)	NMNH	15	E. Africa	tropical rainforest
Litocranius walleri (gerenuk)	NMNH	24	E. Africa	tropical savanna
Intermediate feeders preferring forbs and shrub or tree foliage				
Gazella granti (Grant's gazelle)	NMNH, KNM	40	E. Africa	tropical savanna
Taurotragus oryx (eland)	NMNH, KNM	23	E. Africa	tropical savanna
Fresh grass grazers dependent upon water				
Kobus ellipsiprymnus (common waterbuck)	AMNH	18	E. Africa	tropical savanna
Connochaetes taurinus (wildebeest)	NMNH	26	E. Africa	tropical savanna
Non grazer perissodactyls				
Fruit, dicotyledon foliage, forb, shrub and tree foliage				
Tapirus indicus (Indian tapir)	AMNH	2	Malasia	tropical rainforest
Tapirus terrestris (Brazilian tapir)	AMNH,NMNH	14	S. America	tropical rainforest
Fruit, dicotyledon foliage, forb, shrub and tree foliage, fresh grass				
Tapirus bairdi (Baird's tapir)	AMNH, NMNH	19	S. America	tropical rainforest
Dicotyledon foliage, forb, shrub and tree foliage				
Diceros bicornis (African black rhinoceros)	NMNH	10	E. Africa	tropical savanna-woodland
Fresh grass and roughage grazer				
Equus burchelli (Burchell's zebra)	NMNH	27	E. Africa	tropical savanna

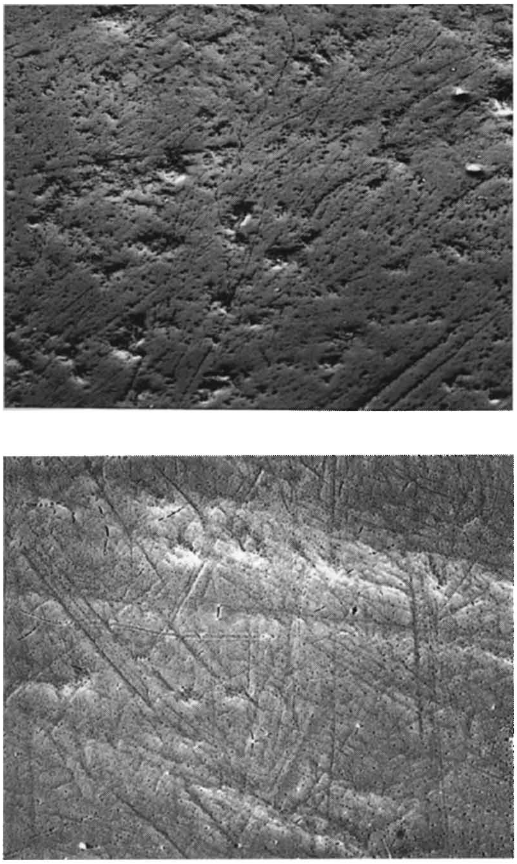

Fig. 1. Representative SEM photomicrograph of tooth microwear recorded on enamel surfaces of extant and extinct species magnified 500 times. Above: *Tapirus indicus* AMNH 8007, a browser. Below: *Cremohipparion proboscideum* AMNH 20272 Quarry X (8.5 Ma) from Samos, Greece.

Microwear data collected on each specimen included observations on the length and width of each feature, as well as a count of the total number of all features found on the surface of the tooth. The ratio of length to width was used to divide the features into the pit and scratch categories. By this procedure we recognized 15 quantifiable variables (see Table 3).

3.3. Quantitative methods

Descriptive, univariate statistics were calculated for each extant and fossil species. Variance homogeneity, at least to some specified level, is a prerequisite for the correct application of an analysis of variance methodology. Therefore, both tests for species level variance homogeneity and for mean values were calculated for the three species groups: extant bovids, extant perissodactyls and fossil hipparions. Univariate post hoc tests were computed across each group of spe-

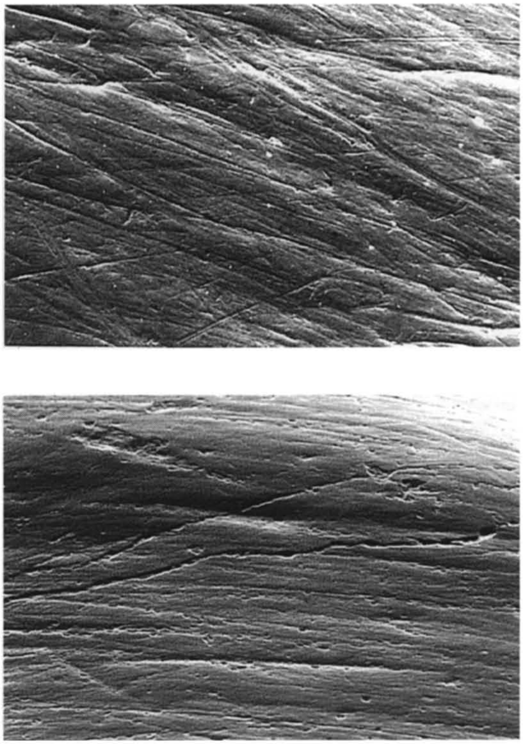

Fig 2. Representative SEM photomicrograph of tooth microwear recorded on enamel surfaces of extant and extinct species magnified 500 times. Above: *Equus burchelli* NMNH 181839, a grazer. Below: *Cormohipparion occidentale* AMNH 71800 (12–8 Ma) North America.

Table 3. Microwear variables.

Total counts of features, pits, scratches	3
Proportion of pits, proportion of scratches	2
Lengths of features, pits, scratches	3
Widths of features, pits, scratches	3
Length : width ratio of features, pits, scratches	3
Total number of pits / number of scratches	1
Total	15

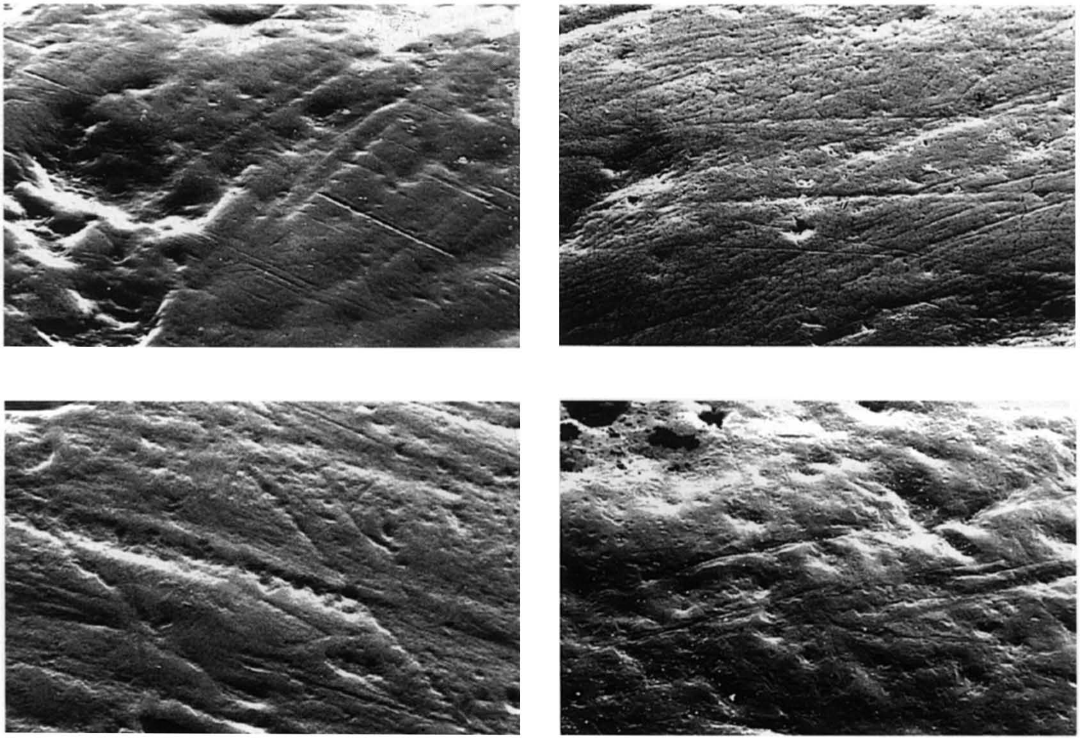

Fig. 3. Representative SEM photomicrograph of tooth microwear recorded on enamel surfaces of extant and fossil species magnified 500 times. Above left: *Tapirus terrestris* NMNH 261025, a browser. Above right: *Tapirus bairdi* AMNH 80075, a browser. Below: *Cormohipparion sphenodus* (14–12 Ma) North America; Left: AMNH 10823, Right: AMNH 71889.

cies after each significant analysis of variance result. In addition, multivariate centroids were examined by means of the Mahalanobis distance measure. Comparisons in the projection space were determined based on the measures of enamel features, scratch and pit lengths, widths and counts. All analyses and descriptive measures were computed using the SPSS PC+ Version 2 on a Compaq 386/20 system.

Extant species were analysed according to their known dietary habits. Significant differences in means and variance homogeneity were tested between dietary categories. Then a perissodactyl model was developed to define, in a probabilistic sense, potential distinctions between the two broad categories "browser" and "grazer". After this 2-group extant perissodactyl model was developed and tested, the same microwear variables measured on the fossil taxa were transformed into the extant perissodactyl model's space by means of Fisher's classification functions. These were calculated to determine the dietary categorization of the hipparion sample relative to the axes for the extant specimens' model.

Similar statistical procedures were performed on the extant bovids. The bovids were first separated into the browsing, intermediate and grazing categories as specified above. Descriptive statistics and tests of means and variance homogeneity were executed. Univariate, parametric post hoc tests were performed to determine the separation probabilities of the pairwise comparisons. An attempt was made to model this three-group division, but only two separate axes were delineated.

Therefore, a two-group model was implemented to describe the dichotomization of the two bovid dietary categorizations, "browsing" and "grazing". Since our research design called for us to characterize the hipparionine horses, for which there are no direct extant descendants, we next chose to develop a joint perissodactyl-bovid model using our entire extant sample. This four group model included:

1) perissodactyl browsers ($n = 45$),
2) perissodactyl grazers ($n = 29$),
3) browsing bovids ($n = 39$), and
4) grazing bovids ($n = 44$).

This model utilized microwear enamel variables judged to be the most discriminating using an F-statistic criterion. As the final step, we employed Fisher's classification functions to transform the fossil hipparion specimens from the raw measure space, to the four-group model space (combined extant perissodactyl-bovid sample).

4. Results

Fourteen of the 15 variables (except the pit count variable) showed statistically significant differences amongst the five extant perissodactyl species. Bartlett's test for variance homogeneity was performed and revealed that only width variability was significantly different across all species. When a test of each variable's mean difference was executed on these five species (each species being allocated to its dietary category of either "browser" or "grazer"), the only variables which showed significant differences in their means were pit length ($P = 0.002$) and width ($P = 0.014$). The variance of enamel overall or total feature widths showed significant heterogeneity when using the standard F test ($P = 0.000$).

We were next interested in uncovering a subset of microwear variables which would maximize species segregation. If it were possible to identify each of the five extant perissodactyl species as a distinct entity, species level variability might overwhelm any attempt to model a quantitative dietary description. Using the Mahalanobis distance measure as a criterion, we found it difficult, but not impossible, to separate all five perissodactyl species. However, *E. burchelli* was not distinguishable from either the tapir or the rhinoceros species until at least eight variables were used together, some of which had doubtful statistical utility for prediction with this model.

The final model showed that the important variables for species segregation were:

a) numbers of pits and scratches,
b) length and width of the pits and scratches,
c) length:width feature ratio, and
d) proportion of pits to scratches.

The functions' standardized weights showed that the proportion of pits to scratches variable accounted for a majority of the system's variability, and was most useful for isolating species. However, overlap of the species statistical sample distributions was extensive and prediction, especially for specimens of E. *burchelli*, was subject to considerable error.

An attempt was then made to model the distinction between the perissodactyl browser and grazer categories. These two groups were found to be separable at the $P = 0.000$ level using only scratch width. However, the distributions overlapped to such a large degree that subsequent prediction became impractical. If we added the pit length measurement as well as the pit counts and the counts and proportion of scratches, we were able to correctly classify 81% of the specimens into the predetermined dietary categories, and explain 66% of the system's variability. The first axis in the model's space was most heavily influenced by pit lengths, as measured by the standardized coefficients.

We then analysed the thirteen hipparion species (Table 1). We calculated means and tested species level variability for those five taxa with sample sizes greater than four (Mi, Cog, Cos, Hdie, Crpro). Variance heterogeneity was detected for feature lengths and widths, and the ratio of these two measurements, across the same five species. The only other variable which showed heteroscedasticity was the length:width scratch ratio. Significant mean differences were detected for the length and width and ratio of the features. However, of those species with sample sizes larger than four, only Cos could be said to be distinct from Cog as well as from Hdie, after post hoc testing. The remainder of the pairwise tests were nonsignificant for these enamel microwear variables. Post hoc tests showed that both pit length:width ratio and proportion of pits showed significant differences across all the five hipparion species.

After initial descriptive statistics were calculated, and preliminary statistical tests were analyzed on extant forms, we submitted the hipparion sample for analysis. The hipparion sample was treated as a group with unknown diet. Hipparion species were assigned to extant perissodactyl categories using the variables which maximized extant dietary separation:

a) pit length and width,
b) pit and scratch counts, and
c) ratio of pits to scratches.

Fig. 4 shows the perissodactyl browser and grazer centroids in the canonical space defining the two-group model. Species means and single taxon representatives of the hipparions are placed for comparison.

Our assignment procedure assumed that the hipparionine horses and extant perissodactyl species used in this analysis had comparable dietary profiles. This assumption can at best be approximate since Miocene vegetation communities were certainly different from those existing today. Note that in some cases in the discussion to follow, the sample sizes do not agree with those stated above; this is due to treatment of missing values.

There were a number of hipparion taxa not definitively assigned to the grazing perissodactyl category. Of the 10 Mi specimens included in this analysis, 6 wère classified as grazers, five with probabilities all above 0.90, and 4 were classified as browsers (2 of 4 had probabilities below 0.6). The 10 specimens of Cos were evenly segregated into grazers or browsers, with probabilities ranging from 0.52 to 0.98 in both categories. The Crpro sample was not well assigned: 3 of the 5 specimens were classified as grazers with probabilities ranging from 0.55 to 0.71; 2 specimens were classified as browsers, having been assigned probabilities of 0.54 and 0.75. Of the two Crmed specimens sampled, one was classified as a browser (0.71 probability), while the other was most similar to the grazing perissodactyls (probability of 0.61). The one Crlic specimen was disputably classified as a browser with a 0.502 probability.

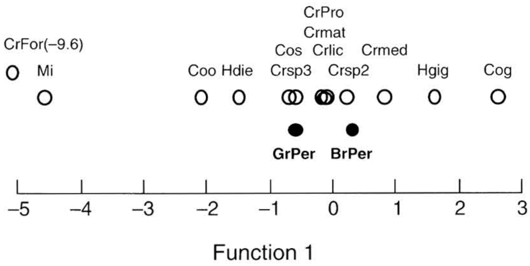

Fig. 4. Plot of Perissodactyl group centroids on the two-group model's canonical axis with comparative placement of hipparion species means.

A number of the hipparion taxa were classified as being most similar to grazers under the perissodactyl 2-group model. Eight of 9 Cog specimens were classified as perissodactyl grazers with relatively high probabilities (0.63–1.00) while one specimen was assigned to the grazing category with a relatively low probability (0.54). Of the 13 Hdie specimens, 12 were determined to be grazers; all but one having classification probabilities over 0.7. One Hdie specimen was denoted a browser, and assigned to that class with the low probability of 0.52 (a value non-significantly different from a chance allocation).

The remaining hipparion species were represented by one or two individuals only. Because we have detected large species level variability, the dietary categorization of these specimens is statistically more questionable. Coo was clearly classified within the grazers, with a 0.89 probability (Fig. 2). The two Hgig specimens were associated with the browsers with high probabilities (0.86 and 0.84). The one specimen of Crmat was only weakly identified as a grazer (0.52 probability). The two specimens of Crsp2 were assigned as a browser and a grazer with 0.68 and 0.53 probability levels, respectively. The two specimens of Crsp3 were both described as grazers (probabilities of 0.56 and 0.72). The one Crfor specimen was strongly categorized a grazer, with a 0.9999 observed probability.

We next considered an assignment of the hipparions according to the 4-group model which included extant perissodactyls and artiodactyls (bovids) jointly. Statistically useful variables proved to be: total number of features, length, width and ratio of the features and the proportion of pits to scratches. Although the ratio of any two variables which have Normal population distributions can not be proved to be Normally distributed, the distributional discrepancy of the feature ratio sample could not be detected by the usual tests. We therefore chose to include this variable in our model. We could not obtain pairwise separation of the two perissodactyl groups until the last variable, feature width, was added to the model. At this juncture, grazing bovids could only be separated from browsing perissodactyls at the P = 0.074 level. We do not consider this to be a well modelled circumstance.

The first canonical correlation indicates that the associated function explains approximately 86% of the variability in the system, while the second explains about 12%. The first function is most heavily weighted by the total number of enamel features, while the second is described

Table 4. Classification of hipparionine horse species within two and four group models (b = browser, g = grazer, B = Bovid, P = Perissodactyl).

Specimen		2-Gr.	P	4-Gr.	P
Merychippus insignis	1	b	0.79	b B	0.39
	2	g	0.999	b B	0.98
	3	g	1.00	b B	0.89
	4	g	1.00	–	–
	5	–	–	–	–
	6	g	0.54	g B	0.62
	7	b	0.60	g B	0.67
	8	g	0.97	g P	0.999
	9	b	0.83	g B	0.63
	10	g	0.91	b B	0.55
	11	b	0.51	g P	0.48
Cormohipparion goorisi	1	g	1.00	g B	1.00
	2	g	0.71	g B	0.33
	3	g	0.54	g P	0.51
	4	g	0.77	g P	0.82
	5	g	0.97	g P	0.95
	6	g	0.71	g P	0.64
	7	g	0.99	g P	0.999
	8	g	0.63	g P	0.38
	9	g	0.81	g P	0.74
Cormohipparion sphenodus	1	b	0.61	b P	0.62
	2	g	0.52	g P	0.47
	3	b	0.54	b B	0.30
	4	g	0.74	g P	0.43
	5	b	0.97	b P	0.59
	6	g	0.98	b B	0.82
	7	g	0.98	g B	0.56
	8	b	0.88	b P	0.44
	9	g	0.80	g P	0.55
	10	g	0.57	g P	0.41
Cormohipparion occidentale	1	g	0.89	g B	0.54
"Hipparion" giganteum	1	b	0.86	b P	0.66
	2	b	0.84	b P	0.33
Hipparion dietrichi	1	g	0.995	b P	0.58
	2	g	0.58	g P	0.93
	3	g	0.92	–	–
	4	g	0.69	b P	0.47
	5	b	0.52	b P	0.75
	6	g	0.61	g B	0.36
	7	g	0.92	g P	0.87
	8	g	0.65	g B	0.37
	9	g	0.67	g P	0.48
	10	g	0.68	–	–
	11	g	0.77	g P	0.62
	12	g	0.65	g P	0.54
	13	g	0.98	–	–
Cremohipparion mediterraneum	1	g	0.60	g P	0.31
	2	b	0.71	b P	0.76
Cremohipparion proboscideum	1	g	0.58	b P	0.39
	2	g	0.55	g P	0.39
	3	g	0.71	g P	0.28
	4	b	0.75	b P	0.47
	5	b	0.54	g P	0.36
Cremohipparion matthewi	1	g	0.52	b P	0.83
Cremohipparion sp. 2	1	b	0.68	g P	0.34
	2	g	0.53	b P	0.31
Cremohipparion sp. 3	1	g	0.56	g P	0.57
	2	g	0.72	g P	0.66
Cremohipparion forsteni	1	g	1.00	–	–
Cremohipparion licenti	1	b	0.502	g P	0.71

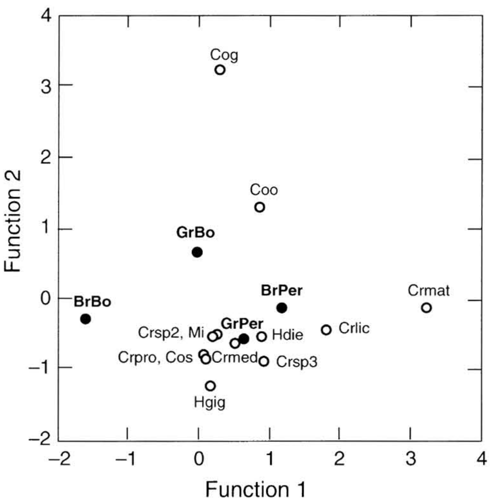

Fig. 5. Plot of grazer and browser Perissodactyls and Bovid browser and grazer group centroids on the first two canonical axes for the 4-group model with placement of hipparion species means.

by the feature length and feature length:width ratio (Fig. 5).

Using this model, we were able to correctly classify on a post-hoc basis: 82% (31 out of 38) of the browsing bovids, 50% (22 of 44) of the grazing bovids, 63% (26 of 41) of the browsing perissodactyls, and 54% (15 of 28) of the grazing perissodactyls. This evidence suggests that the browsing perissodactyls and grazing bovids are statistically indistinguishable for our purposes.

Because this portion of our study included four groups, a probability of 0.25 would correspond to a chance assignment. Compare this with the chance probability of 0.50 above, in which there were two groups.

Under the 4-group model there was a group of species not classified conclusively as grazers. Mi specimens were again classified into both browsing and grazing categories; all but two specimens were most closely related to the extant bovids rather than to the perissodactyls. The Cos sample (Fig. 3) was not consistently assigned under the joint 4-group model; the specimens were about equally classified as browsers or grazers, and with the exception of a single specimen, the assignment to these dietary groups remained the same under this model as under the two-group model. Three of the specimens were placed into the bovid category. The specimen of Crmat which had been designated as a grazing perissodactyl with a probability of only 0.52 with the two-group model, was determined to resemble a browsing perissodactyl with a relatively high probability of 0.83 under this model.

All specimens of Cog were again classified as grazers. However, the first two specimens were more closely identified with the bovids than with the perissodactyls. The single Coo specimen was classified as a grazing bovid with a 0.54 probability (Fig. 2). The Hdie sample contained 10 specimens with four designated as browsers and the remainder as grazers. Of these 10, only two were classified bovids. As with the two group model, all specimens of Crpro (Fig. 1) remained closely related to the extant perissodactyls; 3 specimens categorized as grazers and 2 as browsers. Hgig, Crsp2 and Crsp3 specimens maintained their perissodactyl and dietary classifications with high probabilities. The single Crfor specimen could not be used for this model because of missing data. The single Crlic specimen was categorized as a grazer, with a relatively stronger probability (0.71 in the 4-group model versus 0.502 in the 2-group model).

5. Discussion

In the course of this analysis we uncovered some methodological difficulties with traditionally used microwear variables. We considered the calculation of medians and quartiles because of the wide ranges found in all the measurements. However, no increased precision was found when we applied these statistics. A primary example of such a problem is the statistical definition of a pit. A pit has neither been standardized in past work (see for example Gordon 1982, Teaford & Walker 1984, Grine 1984), nor does it completely reflect the actual range of features a single observer might recognize as a pit (for example Gordon 1982, Grine 1984). Some investigators have used a length:width cutoff point as large as 10. We have found that even a cutoff point of 4, as used in the present study, may be too extreme. An examination of the mathematical properties of the tooth features suggests that a length : width ratio of less than or equal to four actually may be descriptive of more than one entity. Currently accepted practice defines the dichotomization of features into pits and scratches in order to discriminate small, rounded marks from those which appear elongated and directional. When we translated this qualitative description into a mathematical one, it lead to an investigation into the ellipsoid nature of the features. An ellipsoid is one type of conic section for which we can define its eccentricity to be the distance of its center from the axis about which it turns. Then the eccentricity calculation can be used to determine a cutpoint between the two notions of pit and scratch because it equals zero for an exact circular figure and becomes negative for an ellipsoid figure. It appears that when the length: width ratio approaches an asymptote of two, the best generic definition of a pit, as a circular conic, occurs. As the ratio departs from this quantity, the microwear attribute itself appears to change from ellipsoidal to linear. We also found the pit to scratch dichotomy to be too restrictive for describing the greatest potential variation in the system (Solounias & Hayek, in prep.).

Pit width measurement appears to be subject to two major sources of variability: digitization error and the error involved in selection of the point of maximal width along the trajectory of the selected feature. No statistical transformation can reduce this type of variance, and therefore we recommend it not be used for future comparisons until this inherent error can be reduced. When terms have been refined and others added as variables, subsequent analyses will, in all probability, yield more discrete dietary categories. It is interesting to note that when we developed the model for the perissodactyl dietary dichotomy, the most useful set of variables for separation included pit and scratch information. Alternatively, when we combined the perissodactyl and bovid species, the total sample was more highly variable and the definitions of browsing and grazing were then less distinct. For this model the only variables which were found to provide for discrimination of species were those of the total features, not broken into pit and scratch information. We found further procedural problems with determining scratch distributions based upon statistically defined censoring.

With these reservations in mind, we very tentatively make some observations on hipparion diet. Table 1 lists the species used in this study along with the known chronological age range, geographical distribution and facial morphology (facial fossae and nasal retraction). These hipparionine species represent a significant portion of an evolutionary series pertinent to Old World Neogene hipparionine phylogeny (re: Bernor et al. 1989). *Merychippus insignis*, *Cormohipparion goorisi*, *Cormohipparion sphenodus* and *Cormohipparion occidentale* are a North American evolutionary series related either as potential sister (Cos and Coo), or outgroup (Mi and Cog) taxa to the remaining hipparion species in our sample. If one were to adopt accepted dogma that the first occurrence of Old World hipparions marked the first appearance of Old World "savanna-grasslands", then one would predict that somewhere within the North American *Cormohipparion* series we would observe a clear dietary shift to grazing. If one were to adopt the alternative hypothesis explicitly stated by Webb (1983) and implicitly stated by MacFadden & Hulbert (1989), we would believe that all hipparionines, and a significant number of North American high crowned nonhipparionine lineages, were adapted to a grazing regime. The grazing status of high crowned horses has previously been assumed because of their hypsodont morphology. However, Janis (1988) has argued that ungulate hypsodonty does not necessarily correspond to grass eating.

Our data supports Janis' (1988) observation that ungulate hypsodonty does not necessarily correspond to grass eating. A statistically clear grazing morphology occurred only in the 2-group model for Cog, Coo, Hdie, Crmat, Crsp3 and Crfor. In the 4-group model, the clear grazing affinity is maintained only for Cog, Coo and Crsp3. A number of our taxa showed a mixture of browsing and grazing relative to the 2-group model: Mi, Crmed, Crpro, Crsp2. All of these taxa were consistent in maintaining their mixed dietary character in the 4-group model. Hgig and Crlic were the only browsers under the 2-group model, and Crlic was categorized as a grazer with the 4-group model (but note that the low sample sizes for both of these taxa makes their assignment precarious). It should be noted further that when the 4-group model was used, the fossil sample only consistently grouped within order (Perissodactyla) for Crmed, Crmat, Crsp2, Crsp3 and Crlic, all members of a single clade.

We believe that our data is suggestive of a broader dietary preference than mere grazing amongst hipparionines. This is a reasonable assertion given the long chronologic and biogeographic ranges of these equids, and the broad range of habitats that they certainly exploited. Unfortunately, this assertion cannot be directly tested in all cases by paleobotanic and taphonomic data. There are, however, some phylogenetic and morphologic parallels which allow us to pose a scenario suitable for future testing.

The most primitive taxon under consideration, Mi (a non-hipparionine), is believed to be the sister taxon of Cog, the most primitive hipparion (refer here to Bernor et al. 1989 for this particular argument). Mi shows a combination of browsing and grazing. The oldest known hipparions, Cog (ca. 15 Ma), as well as the later North American taxon belonging to this clade, Coo (ca. 12–8 Ma), are strongly categorized as grazers; an intermediate stage of evolution, Cos, exhibits a mixed diet. This evidence suggests that grazing, as defined by our tests, was probably a means by which these North American equids obtained a significant portion of their diets. This data agrees well with Webb's (1983) observations that Middle and Late Miocene North America underwent an environmental shift to more open country "savanna-like" habitats, and that hipparionine (and other) equids developed for at least some grazing habits. However, based on our preliminary data we believe that it is distinctly possible that Webb's (1983:fig. 5, p. 285) mixed dietary category was taxonomically broader than he originally estimated. This hypothesis should be specifically tested in subsequent studies.

As a group, Old World hipparions show mixed "browsing" and "grazing". This can be predicted by independent paleoenvironmental data when taking into account Bernor's (1983, 1984) and Bernor et al.'s (1979, 1992) observations that Old World later Neogene localities show strong regional provinciality which includes patchy distributions of open country and more forested habitats. Of those Old World taxa that show clear grazing patterns under the 2-group model (Hdie, Crmat, Crsp3 and Crfor), all are species which have significantly reduced or lost their facial fossae compared to some other members of their clade. Those taxa which exhibit either a mixed diet or a clear utilization of browse, have retained (Hgig), or elaborated (Crmed, Crpro and Crlic), their facial fossae structures compared to some members of their own lineages.

The observation that there is a potential relationship between hipparionine facial morphology and diet is an important component of any future testing with this group. Hgig and Hdie are taxa with a single dorsal preorbital fossa and well developed buccinator fossa; the former is placed in the area of origin for the levator labii superioris muscle, the latter in the area of origin for the buccinator muscle (of extant *Equus*; also see Zhegallo 1978:fig. 17, p. 39). The *Cremohipparion* genus group has in all but three species (*C. moldavicum*, *C. nikosi* and *C. matthewi*), three discernable facial fossae: dorsal preorbital, intermediate (= caninus) and buccinator. The dorsal preorbital and buccinator fossae are believed to have the same muscle origins as those cited above, whereas the intermediate is believed to be the site of origin for the caninus muscle. We hypothesize here that the elaboration of these facial structures, along with their well developed musculature and strong nasal retraction (as seen in Crmed, Crpro, Crlic), reflects the development of a short proboscis, or at the least a very large and mobile lip. Such a highly mobile lip (or proboscis) was even more mobile than that seen in extant *Equus*, and may have served to gather a broad range of vegetation, including both grass and browse. Today the elephant, which has a proboscis, eats grass. Tapirs also have probosci, but browse. Those *Cremohipparion* species which had well developed facial fossae may have had probosci which we propose to have been used for gathering mixed browse and graze vegetation. We assert that the assortment of the hipparion statistical dietary categorizations cited here reflects a broader diet than simple grass eating. Further discrimination within and between these species is mandatory to more clearly distinguish the range of dietary preferences for the *Cremohipparion* clade. We see this as one additional important direction for future research.

6. Conclusions

We have attempted here to characterize the diet of some selected hipparionine horses. Based upon an analysis of tooth microwear features, a statistical strategy was developed to invoke dietary categorization. Dietary evaluation was then viewed in light of reported paleobotanic, phylogenetic and morphologic information. The statistical evidence lead us to conclude that the 13 hipparion species in our sample, which represent a segment of their North American and Eurasian record, did not adhere strictly to a definitive grass diet. We have identified certain methodological aspects which are in need of refinement and outlined our approach for future work, for example, the dichotomization into pit and scratch categories as based upon a consolidation of mathematical and qualitative descriptors, and an evaluation of the use of such a dichotomized scale versus the advantage of continuous measurement. Our statistical approach has the potential to provide much additional information concerning both recent and fossil species.

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