THOMAS M. KAISER, NIKOS SOLOUNIAS, MIKAEL FORTELIUS, RAYMOND L. BERNOR & FRIEDEMANN SCHRENK

Tooth mesowear analysis on *Hippotherium primigenium* from the Vallesian Dinotheriensande (Germany) – A blind test study

Abstract
A new approach of reconstructing ungulate diet, the mesowear method was recently introduced by FORTELIUS & SOLOUNIAS (in press). Expressions of tooth wear were found to have strong diagnostic capabilities for ungulate diets. The present study is the first test of the mesowear method in two ways: (1) to reconstruct the dietary regime of *Hippotherium primigenium,* an equid from the Vallesian Dinotheriensande (Germany) applying the mesowear method; (2) to test the robustness of the mesowear method by applying a blind test approach where several researchers scored the same sample of teeth independently of each other. As a consensus dietary diagnosis for *Hippotherium primigenium*, a mixed diet with grassy components similar to the diet of the impala (*Aepyceros melampus*) is suggested. We find the mesowear method to be efficient and robust.

Kurzfassung
Paläodiät-Analyse an *Hippotherium primigenium* aus den vallesischen Dinotheriensanden (Rheinhessen) mit der Mesowearmethode – eine Blindteststudie
Ein neuer Ansatz zur Rekonstruktion der Paläodiät von Huftieren, die Mesowearmethode, wurde kürzlich von FORTELIUS & SOLOUNIAS (im Druck) beschrieben. Ein großes diagnostisches Potential für die Ernährungsweise von Huftieren wurde in Merkmalen der Zahnabnutzung auf der Okklusalfläche erkannt. Die vorliegende Untersuchung ist in zweifacher Hinsicht der erste Test der Mesowearmethode. (1) Es wird die Diät des hipparionten Equiden *Hippotherium primigenium* aus den vallesischen Dinotheriensanden (Rheinhessen, Deutschland) unter Anwendung der Mesowearmethode rekonstruiert. (2) Um die Robustheit der Methode zu überprüfen, wird eine Blindteststudie durchgeführt, in der die 5 Autoren dieselbe Sammlung oberer zweiter Molaren unabhängig voneinander untersuchen. Als Konsensusdiät für *Hippotherium primigenium*, wird eine gemischte Nahrungszusammensetzung mit Grasanteil, ähnlich der des Impala (*Aepyceros melampus*) vorgeschlagen. Die Mesowearmethode hat sich als effektiv und robust erwiesen.

Autoren
Dr. THOMAS M. KAISER, Institute and Museum of Zoology, University of Greifswald, D-17489 Greifswald, Germany; e-mail: kaiser@mail.uni-greifswald.de.
Prof. Dr. NIKOS SOLOUNIAS, Department of Anatomy, New York College of Osteopathic Medicine, of the New York Institute of Technology, Old Westbury, NY 11568 8000, USA; e-mail: nsolouni@iris.nyit.edu
Prof. Dr. MIKAEL FORTELIUS, Department of Geology, Division of Geology and Paleontology, PO Box 11, FIN 00014 University of Helsinki, Finland; e-mail: mikael.fortelius@helsinki.fi
Prof. Dr. RAYMOND L. BERNOR, College of Medicine, Department of Anatomy, Laboratory of Evolutionary Biology, Howard University, 520 W St. N.W., Washington D.C. 20059, USA; e-mail: raybernor@compuserve.com
Prof. Dr. FRIEDEMANN SCHRENK, Department of Geology, Mineralogy and Paleontology, Hessia State Museum, Friedensplatz 1, D-64289 Darmstadt, Germany; e-mail: friedemann.schrenk@hlmd.tu-darmstadt.de

Introduction

Reconstructing the dietary adaptation of fossil ungulates is expected to provide important information on the adaptation of individual species and ultimately on habitat conditions of terrestrial mammalian paleocomunities. Previous attempts with similar aims have been undertaken using a wide variety of methods, which include stable isotope abundances (MACFADDEN et al. 1996, 1999) and tooth microwear analysis of the occlusal surface of tooth enamel (HAYEK et al. 1992, SOLOUNIAS & HAYEK 1993, SOLOUNIAS & MOELLEKEN 1993). TEAFORD (1988) and JANIS (1995) have reviewed microwear research. In addition, tooth crown height analysis (JANIS 1988), and masseteric morphology analysis (SOLOUNIAS & MOELLEKEN 1993, SOLOUNIAS & DAWSON-SAUNDERS 1988) have also been used to interpret paleodiets. All methods applied so far, however, have proven relatively laborious, restricting studies to small sample size.
A new approach of reconstructing ungulate diet, the mesowear method was recently introduced by FORTELIUS & SOLOUNIAS (in press). Mesowear is based on facet development on the occlusal surfaces of the teeth. The degree of facet development reflects the relative proportions of tooth to tooth contact (attrition) and food to tooth contact (abrasion), attrition creating facets and abrasion obliterating them. The entire surface of the teeth is affected by tooth wear but mesowear analysis so far has focused on the buccal cutting edges of the enamel surfaces where the buccal wall (ectoloph) meets the occlusal plane. There, mesowear was simply defined as cusp relief and cusp shape in buccal (lateral) view. These simple expressions of tooth wear were found to have strong diagnostic capabilities for ungulate diets (FORTELIUS & SOLOUNIAS, in

press). The aim of the present study is the first test of the mesowear method in two ways: (1) to reconstruct the dietary regime of the hipparionine equid *Hippotherium primigenium* from the Vallesian Dinotheriensande (Germany) applying the mesowear method; (2) to test the robustness of the mesowear method. For this, we favored a blind test approach where five researchers scored the same teeth independently of each other. A large sample of teeth of *H. primigenium* was selected for this purpose.

Hipparionine horses are ideal for application of the mesowear method because of a number of attributes intrinsic to the group, including: their abundance in the Holarctic and Ethiopian later Neogene mammal faunas, their species diversity and their long geographic and chronologic ranges. Moreover, hipparionine horses are morphologically diverse and, according to recent analyses of the cranial, dental and postcranial anatomy, are found to have been adapted to a broad range of habitats and feeding adaptations (re: BERNOR et al. 1989; BERNOR & ARMOUR-CHELU 1999, EISENMANN & SONDAAR 1999). These include taxa which were open country grazers of such widely disparate lineages as members of North American *Cormohipparion* and Old World taxa including *Cremohipparion matthewi, Hipparion dietrichi* and *Eurygnathohippus cornelianus.* Central European late Miocene age *Hippotherium primigenium* and its ancestor *Hippotherium sumegense* lived in warm temperate mesophytic forests (BERNOR et al. 1988) and showed both locomotor (BERNOR et al. 1997) and dietary adaptations (BERNOR et al. 1999) that suited them well for their forest habitats. The Dinotheriensande sample of *Hippotherium primigenium* is the largest and best one in Central Europe

Table 1. List of specimens sorted by decreasing crown height (# 1-20 refers to object numbers in Figure 1).

#	Museum	Spec-Id	Locality	Tooth	Side	M1	M3	M5	DT	VD	I(r)	OR hP (1)	CS hP (1)	OR hP (2)	CS hP (2)	OR hP (3)	CS hP (3)	OR hP (4)	CS hP (4)	OR hP (5)	CS hP (5)	OR hP C	CS hP C
1	HLMD	DIN2659	ES	M2	L	23,1	15,8	53,8	12,1	2,7	0,12	h	s	h	s	h	s	h	s	h	s	h	s
2	HLMD	DIN2948	K	M2	R	23,3		51,9	11,2	2,9	0,12	h		h	s	h	s	h	r	h	s	h	s
3	HLMD	DIN2815	EP	M2	L	25,2	21,8	50,2	11,3	2,3	0,09	h		h		h		l	r	h		h	
4	HLMD	DIN2760	EP	M2	L	26,0	23,3	49,6	11,4	2,9	0,11	h		h		h		h	r	h		h	
5	HLMD	DIN3175	W	M2	R	24,9	21,4	47,1	11,9	2,9	0,12	h		h		h		h	r	h		h	
6	HLMD	DIN3177	W	M2	R	24,1	23,4	46,1	12,8	2,4	0,10	h		l		l		l	s	h		l	
7	HLMD	DIN2701	ES	M2	R	25,2	23,5	45,6	13,4	3,6	0,14	h		h		h		h	r	h		h	
8	HLMD	DIN2757	EP	M2	R	25,5	21,7	45,3	12,1	3,7	0,14	h		h		h		h		h		h	
9	SMF	M1430	EP	M2	L	24,1	23,5	44,3	12,2	1,6	0,06	h		l		l		h		h		h	
10	HLMD	DIN3176	W	M2	R	24,4		43,7	11,5	3,2	0,13	h		h		h		h		h		h	
11	HLMD	DIN2860	WO	M2	L	23,2	20,5	40,2	9,4	2,8	0,12	h		h		h		h		h		h	
12	HLMD	DIN2763	EP	M2	L	24,1	22,9	39,4	11,2	1,7	0,07	h		h		h		h		h		h	
13	HLMD	DIN2917	D	M2	L	20,9	19,9	33,1	12,0	2,4	0,12	h		h		h		l		h		h	
14	HLMD	DIN2716	EP	M2	R	22,7	21,5	32,0	11,7	3,1	0,14	h		h		h		h		h		h	
15	HLMD	DIN2711	ES	M2	R	22,8	22,0	30,6	11,8	2,7	0,12	h		h		h		h		h		h	
16	HLMD	DIN1076	DS	M2	L	23,6	23,2	28,5	11,4	1,6	0,07	h		l		l		h		h		h	
17	HLMD	DIN2761	EP	M2	R	22,5	23,1	26,8	12,7	2,4	0,11	h		h		h		h		h		h	
18	SMF	PW1998/ 10048-LS	EP	M2	L	24,2	20,5	24,9	11,4	2,4	0,10	h		h		h		l		h		h	
19	HLMD	DIN2742	ES	M2	L	21,3	23,8	23,4	13,7	2,6	0,12	h		h	b	h		l		h		h	
20	HLMD	DIN2683	EP	M2	R	25,9	20,4		13,5	3,1	0,12	h		h	r	h		h		h		h	

HLMD = Hessisches Landesmuseum, Darmstadt, SMF = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt. Locality abbreviations: D = Dintesheim, DS = Dinotheriensande (no locality specified), EP = Eppelsheim, ES = Esselborn, K = Kettenheim, W = Westhofen, WI = Wissberg, WO = Wolfsheim.
L = left, R = right. M1 = occlusal length, M3 = occlusal width, M5 = mesostyle height (re: EISENMANN et al. 1988 and BERNOR et al. 1997). DT = Distance between cusp tips formed by labial band of protocone and metacone. VD = Distance between line connecting tip formed by labial band of protocone and metacone and bottom of valley between cusp tips. I(r) = VD/M1.
Mesowear variables: OR = Occlusal Relief, CS = Cusp Shape. hP = *Hippotherium primigenium,* Numbers in brackets hP(1)-(5) indicate investigator scoring. C = consensus. Variables are: l = low, h = high , s = sharp, r = round, b = blunt, ? = uncertain diagnosis (excluded from study).

Table 2. Mesowear variable distribution in the datasets hP1-hP5.

Dataset	n	l	h	s	r	b	perlow	perhigh	persharp	perround	perblunt
hP1	20	0	20	7	13	0	0	100	35	65	0
hP2	20	3	17	5	11	1	15	85	29	65	6
hP3	20	3	17	7	13	0	15	85	35	65	0
hP4	20	5	15	8	12	0	25	75	40	60	0
hP5	20	0	20	7	13	0	0	100	35	65	0
C	20	1	19	8	12	0	5	95	40	60	0
M	20	2,2	17,8	6,8	12,4	0,2	11	89	35	64	1

Mesowear variables: l = low, h = high , s = sharp, r = round, b = blunt, C = consensus, M = mean. Perlow = percent low occlusal relief, perhigh = percent high occlusal relief, persharp = percent sharp cusps, perround = percent rounded cusps, perblunt = percent blunt cusps.

for establishing the paleodietary adaptation of this species, and is of further use in calibrating potential observer error in scoring mesowear traits.

The Mesowear Method

The mesowear method as introduced by FORTELIUS & SOLOUNIAS (in press) treats ungulate tooth mesowear as two variables: occlusal relief and cusp shape (Figure 1). Teeth are inspected at close range, using a hand lens when appropriate. The sharper buccal cusp of the second upper molar (either the paracone or the metacone) is scored. Occlusal relief (OR) is classified as high (h) or low (l), depending on how high the cusps rise above the valley between them. In borderline cases a quantitative index is 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. For selenodont forms and plagiolophodont equids, the limit between high and low is arbitrarily set at 0.1, for hyracoids at 0.05, and for rhinoceroses at 0.03. These values are calibrated by the relief observed in the species included in the study, to separate the subjectively "low" from the subjectively "high" taxa. Occlusal relief is used in the analyses as percentages perhigh and perlow (Table 2).
The second mesowear variable, cusp shape, includes 3 scored attributes: sharp (s), round (r) and blunt (b) according to the degree of facet development. A sharp cusp terminates to a point and has practically no rounded area between the mesial and distal phase I facets, a rounded cusp has a distinctly rounded tip (apex) 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 2 as the three variables persharp, perround and perblunt.

Materials and Methods

In order to be consistent, FORTELIUS & SOLOUNIAS restricted their study of ungulate mesowear to upper second molars. We have followed this methodology in selecting all verifiable M2's of Dinotheriensande *Hippotherium primigenium*, 20 in total, currently known. The chronologic homogeneity of this sample, which includes several localities, is uncertain, but there is no reason to believe at present that more than one species is present in this sample. The Dinotheriensande localities are all placed within the lower part of MN 9, the age of which is believed to be about 10.5 Ma. (STEININGER et al. 1996; ANDREWS & BERNOR 1999). Besides being the largest sample of teeth known for *Hippotherium primigenium*, this sample is known entirely from isolated teeth allowing height measurements to be taken which is important for ultimately knowing the wear stage and age of the individual at death.
The tooth crowns of all specimens were moulded with Provil Soft dental moulding putty (Bayer). A set of five epoxy resin casts was made using Injektionsharz EP epoxy resin (Reckli). All scoring was done using plastic casts rather then the original specimens in order to stay consistent with the original method. Furthermore we believe that casts will become an important tool for large-scale investigations applying the mesowear method.

Table 3. Hypsodonty index (hypind) of *Hippotherium primigenium* calculated after JANIS (1988) as tooth height divided by m3 width. M = mean.

Hypsodonty Index after JANIS (1988)				
Spec-Id	Tooth	height	width	hypind
HLMDDIN1078	m3	42,7	10,0	4,26
HLMDDIN2503	m3	49,1	9,0	5,47
HLMDDIN2507	m3	44,9	10,3	4,38
HLMDDIN2522	m3	41,8	9,8	4,26
HLMDDIN2727	m3	48,8	10,8	4,52
HLMDDIN2956	m3	44,3	9,9	4,49
HLMDDIN2931	m3	48,1	8,2	5,84
HLMDDIN2985	m3	49,4	9,9	4,99
HLMDDIN3017	m3	51,7	9,0	5,72
HLMDDIN3178	m3	42,1	9,9	4,25
M		46,3	9,7	4,78

Table 4. The recent and fossil species in this study. sym = abbreviations used to label species in cluster plots. Dietary classification follows the conservative classification of FORTELIUS & SOLOUNIAS (in press).

sym	species	common name	Order	Family
browsers				
AA	*Alces alces*	moose	Artiodactyla	Cervidae
EI	*Ammodorcas clarkei*	dibatag	Artiodactyla	Bovidae
AM	*Antilocapra americana*	pronghorn	Artiodactyla	Antilocapridae
BE	*Boocercus euryceros*	bongo	Artiodactyla	Bovidae
DB	*Diceros bicornis*	black rhinoceros	Perissodactyla	Rhinocerotidae
DS	*Dicerorhinus sumatrensis*	Sumatran rhinoceros	Perissodactyla	Rhinocerotidae
EI	*Ammodorcas clarkei*	dibatag	Artiodactyla	Bovidae
GC	*Giraffa camelopardalis*	giraffe	Artiodactyla	Giraffidae
LW	*Litocranius walleri*	gerenuk	Artiodactyla	Bovidae
OH	*Odocoileus hemionus*	mule deer	Artiodactyla	Cervidae
OJ	*Okapia johnstoni*	okapi	Artiodactyla	Giraffidae
OL	*Capreolus capreolus*	roe deer	Artiodactyla	Cervidae
OV	*Odocoileus virginianus*	white-tailed deer	Artiodactyla	Cervidae
RS	*Rhinoceros sondaicus*	Javan rhinoceros	Perissodactyla	Rhinocerotidae
TT	*Tragelaphus strepsiceros*	greater kudu	Artiodactyla	Bovidae
grazers				
ab	*Alcelaphus buselaphus*	hartebeest	Artiodactyla	Bovidae
al	*Alcelaphus lichtensteinii*	Lichtenstein's hartebeest	Artiodactyla	Bovidae
bb	*Bison bison*	American plains bison	Artiodactyla	Bovidae
cs	*Ceratotherium simum*	white rhinoceros	Perissodactyla	Rhinocerotidae
ct	*Connochaetes taurinus*	wildebeest	Artiodactyla	Bovidae
dl	*Damaliscus lunatus*	topi	Artiodactyla	Bovidae
eb	*Equus burchelli*	Burchell's zebra	Perissodactyla	Equidae
eg	*Equus grevyi*	Grevy's zebra	Perissodactyla	Equidae
he	*Hippotragus equinus*	roan antelope	Artiodactyla	Bovidae
hn	*Hippotragus niger*	sable antelope	Artiodactyla	Bovidae
ke	*Kobus ellipsiprymnus*	common waterbuck	Artiodactyla	Bovidae
rr	*Redunca redunca*	bohor reedbuck	Artiodactyla	Bovidae
mixed feeders				
Ap	*Axis porcinus*	hog deer	Artiodactyla	Cervidae
Ax	*Axis axis*	chital	Artiodactyla	Cervidae
Bt	*Budorcas taxicolor*	takin	Artiodactyla	Bovidae
Ca	*Carpicornis sumatraensis*	serow	Artiodactyla	Bovidae
Cc	*Cervus canadensis*	wapiti	Artiodactyla	Cervidae
Cd	*Cervus duvauceli*	barashingha	Artiodactyla	Cervidae
Ci	*Capra ibex*	ibex	Artiodactyla	Bovidae
Cl	*Camelus dromedarius*	dromedary	Artiodactyla	Camelidae
Cu	*Cervus unicolor*	sambar	Artiodactyla	Cervidae
Gg	*Gazella granti*	Grant's gazelle	Artiodactyla	Bovidae
Gt	*Gazella thomsoni*	Thomson's gazelle	Artiodactyla	Bovidae
Lg	*Lama glama*	llama	Artiodactyla	Camelidae
Lv	*Lama vicugna*	vicugna	Artiodactyla	Camelidae
Ma	*Antidorcas marsupialis*	springbuck	Artiodactyla	Bovidae
Me	*Aepyceros melampus*	impala	Artiodactyla	Bovidae
Oc	*Ovis canadensis*	bighorn sheep	Artiodactyla	Bovidae
Om	*Ovibos moschatus*	muskox	Artiodactyla	Bovidae
Oo	*Ourebia ourebi*	oribi	Artiodactyla	Bovidae
Rf	*Redunca fulvorufula*	mountain reedbuck	Artiodactyla	Bovidae
Ru	*Rhinoceros unicornis*	Indian rhinoceros	Perissodactyla	Rhinocerotidae
Sc	*Syncerus caffer*	African buffalo	Artiodactyla	Bovidae
St	*Saiga tatarica*	saiga	Artiodactyla	Bovidae
Ta	*Tragelaphus angasi*	nyala	Artiodactyla	Bovidae

sym	species	common name	Order	Family
mixed feeders				
Ti	*Tragelaphus imberbis*	lesser kudu	Artiodactyla	Bovidae
To	*Taurotragus oryx*	eland	Artiodactyla	Bovidae
Tq	*Tetracerus quadricornis*	chousingha	Artiodactyla	Bovidae
Tr	*Boselaphus tragocamelus*	nilgai	Artiodactyla	Bovidae
Ts	*Tragelaphus scriptus*	bushbuck	Artiodactyla	Bovidae
extinct species				
cG	*Cormohipparion goorisi*		Perissodactyla	Equidae
cP	*Cremohipparion proboscideum*		Perissodactyla	Equidae
cQ	*Cormohipparion quinni*		Perissodactyla	Equidae
cR	*Pachytragus crassiciornis*		Artiodactyla	Bovidae
hP	*Hippotherium primigenium*		Perissodactyla	Equidae
mI	*Merychippus insignis*		Perissodactyla	Equidae
pL	*Pachytragus laticeps*		Artiodactyla	Bovidae

Each of us recorded the same sample of fossil tooth specimens (Table 1), scoring mesowear features according to the convention introduced by FORTELIUS & SOLOUNIAS. We collected data on teeth of medium wear stages; that is we excluded specimens that were either unworn or worn to less then 20 mm mesostyle height. A total of 20 specimens were used in this study for statistical analysis. As a matter of anonymity, we refer to the individual datasets as hP1-hP5, the sequence of which is random.

All measurements are taken twice using dial calipers, averaged and rounded to 0.1 mm. Molar crown high, occlusal length and width were measured according to the conventions of EISENMANN et al. (1988) and BERNOR et al. (1997). The hypsodonty index for *Hippotherium primigenium* from the Dinotheriensande was calculated according to JANIS (1988). We therefore referred to the lower m3 sample of the Dinotheriensande curated at the HLMD (Table 3).

The distance between a line connecting two adjacent cusp tips (DT) and the deepest point of the valley between is measured as valley depth (DV). DV is divided by the occlusal length of the tooth measured according to BERNOR et al. (1997), giving the occlusal relief Index I(r) (Table 1). Photographed specimens were coated with ammonium chloride to reduce colour contrasts. Photographs are taken with a KONTRON 3012 (CARL ZEISS JENA) digital camera.

FORTELIUS & SOLOUNIAS (in press) used 64 ungulate species in their analyses. Among these were species with variously problematic diets (namely the water chevrotain, the duikers and the hyraxes, which were grouped together – the "mabra" group of "minute abraded brachydont"). These species were excluded in the present study. In addition we presently include 6 fossil bovid and equid species (Table 4) in addition to the 7 experimental datasets of *Hippotherium primigenium* to investigate the dietary classification of *H. primigenium* in relation to these species. Analysis is also undertaken using a reduced set of 27 "typical" recent species as a comparative set, which have been shown to provide reliable dietary data without anomalies.

FORTELIUS & SOLOUNIAS (in press) found that for the 64 living species they investigated in their mesowear study, the single variable that classified the species best was the index of hypsodonty (hypind) and the resolution of the method increased as additional variables were included. We therefore independently included the index of hypsodonty (from JANIS 1988) into this study and use it as an additional variable besides of the mesowear variables.

Of the several dietary classifications FORTELIUS & SOLOUNIAS tested, the conservative classification resulted in the most correct classification of species based on mesowear variables and the index of hypsodonty. We follow their classification of extant species into the three broad dietary categories: browser, mixed feeder and grazer (Table 4).

Statistics

The Chi square test was used to test significant differences between individual data set scores. Hierarchical cluster analysis was applied, with complete linkage (to enhance the distinctiveness of clusters), using three mesowear variables (perhigh, persharp and perround) with and without the index of hypsodonty (hypind) after JANIS (1988). For this analysis we use the original dataset of FORTELIUS & SOLOUNIAS (in press) and the data presented in this study for *Hippotherium primigenium.* All statistical tests were calculated using Systat 5.0 and 7.0 using the default settings.

Results

Occlusal relief was scored high in 75 (hP4) to 100% (hP1 and hP5). All investigators scored more specimens high than low. Cusp shape scorings ranged between 29% (hP2) and 40% (hP4) sharp, 60% (hP4) and 65% (hP1, hP2, hP3, hP5) round and 0% (hP1, hP3, hP4, hP5) to 6% (hP2) blunt (Table 2, Figure 1). All investigators scored more specimens round than sharp, and more sharp than blunt. In the consensus dataset, 5% are low, 95% high, 40% sharp, 60% round and no specimens are blunt. The mean dataset has 11% low, 89% high, 35% sharp, 64% round and 1% blunt.

Chi square analysis of the cusp shape distribution of all five individual datasets (hP1-hP5) indicates no significant differences in the results of the five investigators (P=0.751). The probability is (P=0.724) if the comparison is restricted to hP1-hP3, hP5 which indicates that these datasets are closer, but hP4 is more different. The probability of differences in occlusal relief scorings is (P=0.048). It becomes slightly more insig-

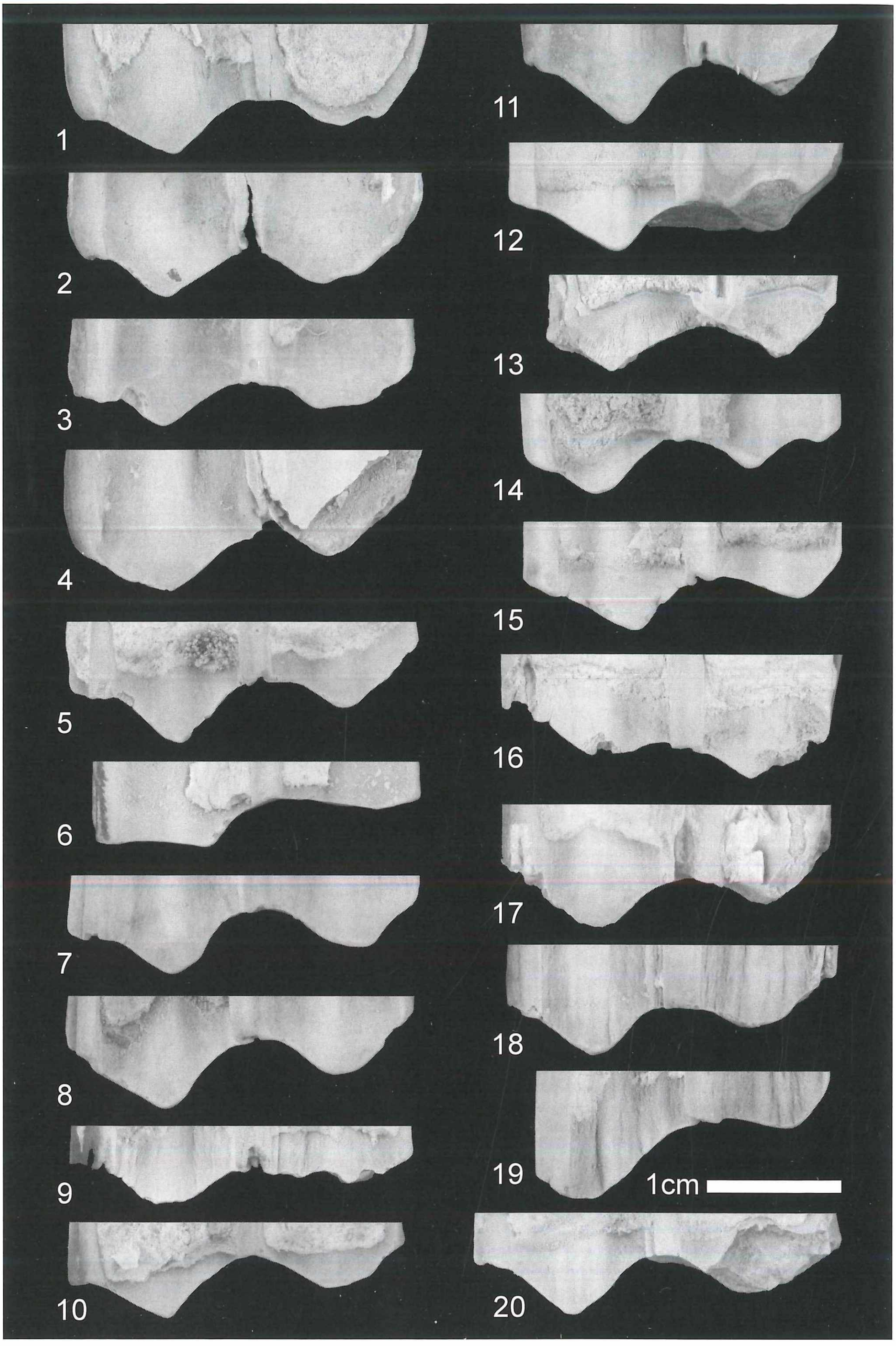

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
1cm

Figure 1. Buccal aspect of the ectolophs of 20 M2 of *Hippotherium primigenium* from the Valesian of Rheinhessen showing the mesowear pattern. With the exception of specimen HLMDDIN2683 (Nr. 20), which does not allow accurate crown height measurement, all specimens are sorted by crown height according to the sequence in Table1. Images of right specimens (d) are mirrored horizontally. Left is mesial.
1) M2s, HLMD DIN 2659,
2) M2d, HLMD DIN 2948,
3) M2s, HLMD DIN 2815,
4) M2s, HLMD DIN 2760,
5) M2d, HLMD DIN 3175,
6) M2d, HLMD DIN 3177,
7) M2d, HLMD DIN 2701,
8) M2d, HLMD DIN 2757,
9) M2s, SMF M1430,
10) M2d, HLMD DIN 3176,
11) M2s, HLMD DIN 2860,
12) M2s, HLMD DIN 2763,
13) M2s, HLMD DIN 2917,
14) M2d, HLMD DIN 2716,
15) M2d, HLMD DIN 2711,
16) M2s, HLMD DIN 1076,
17) M2d, HLMD DIN 2761,
18) M2s, SMF PW1998 / 10048-LS,
19) M2s, HLMD DIN 2742,
20) M2d, HLMD DIN 2683.

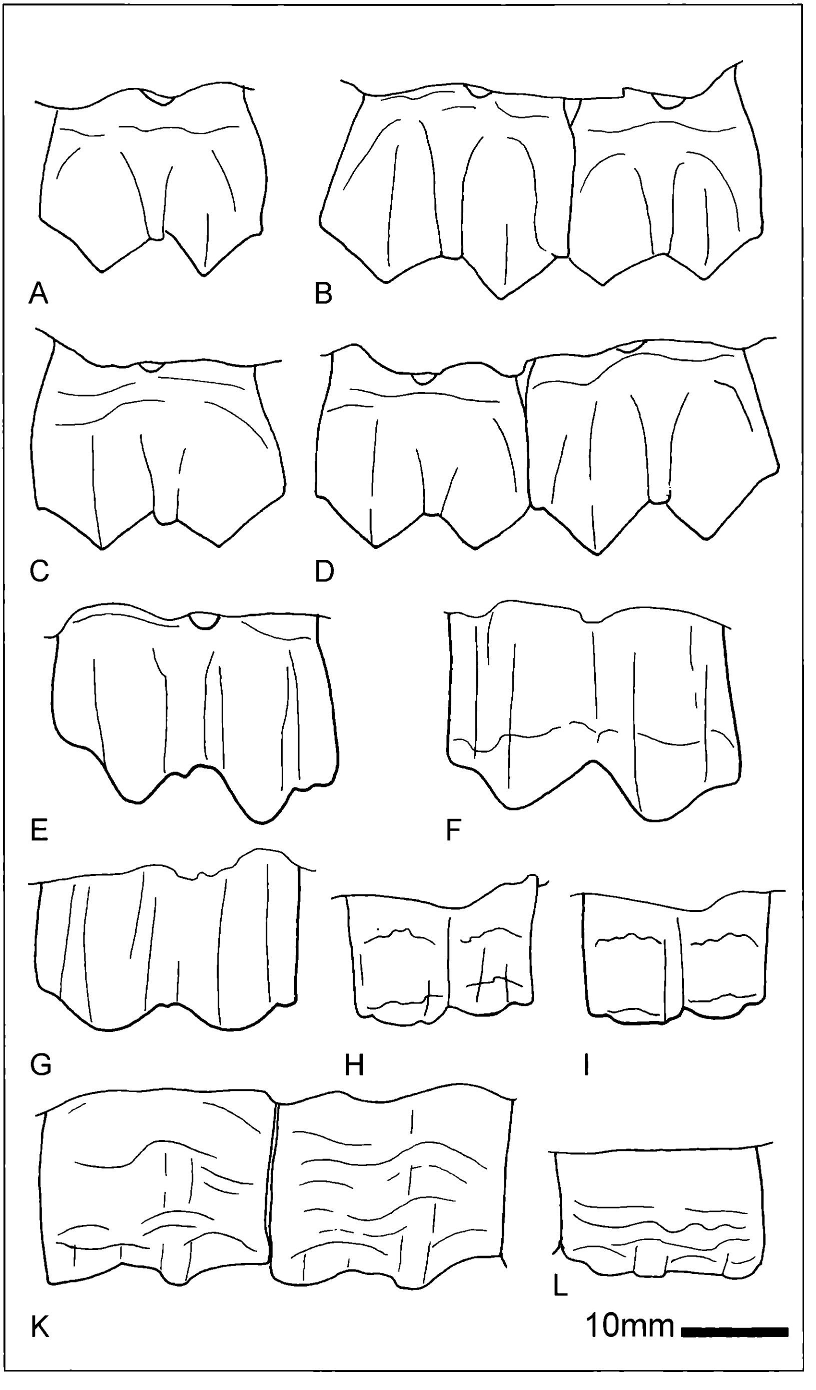


Figure 2. Examples of mesowear. Buccal views of upper molars. A-D: Relief high, Sharp cusps, E-F: Relief high, Round cusps, G: Relief low, Round cusps, H-I: Relief low, Blunt cusps. A) *Alces alces* left M1, AMNH 2077505; B) *Alces alces* left M2-M3, AMNH 6408; C) *Alces alces* right M2, AMNH 19799; D) *Alces alces* right M2-M3, AMNH 98162; E) *Kobus ellipsiprymnus* right M2, AMNH 53496; F) *Alcelaphus buselaphus* right M2, AMNH 31797; G) *Alcelaphus buselaphus* right M2, AMNH 216384; H) *Damaliscus lunatus* right M1, AMNH 82150, I) *Damaliscus lunatus* right M1, AMNH 82144; K) *Equus burchelli* left M1-M2, AMNH 82313; L) *Equus burchelli* right M2, AMNH 27749. AMNH = American Museum of Natural History, New York.

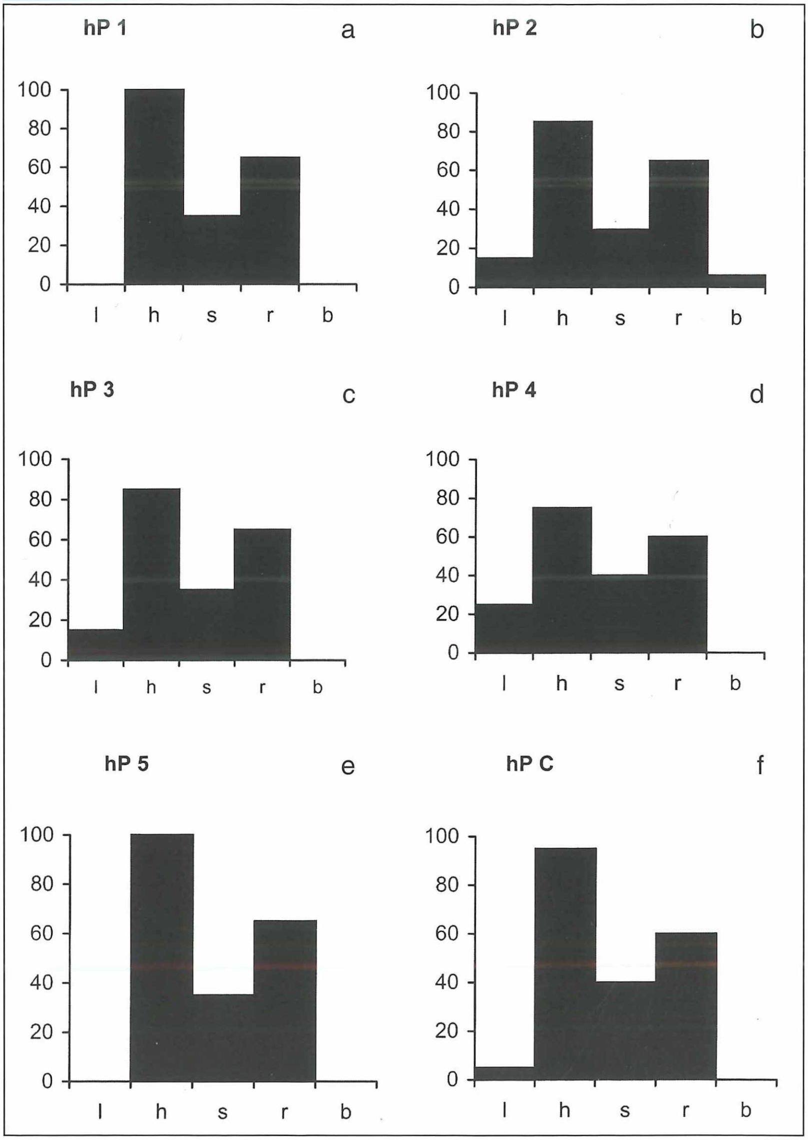
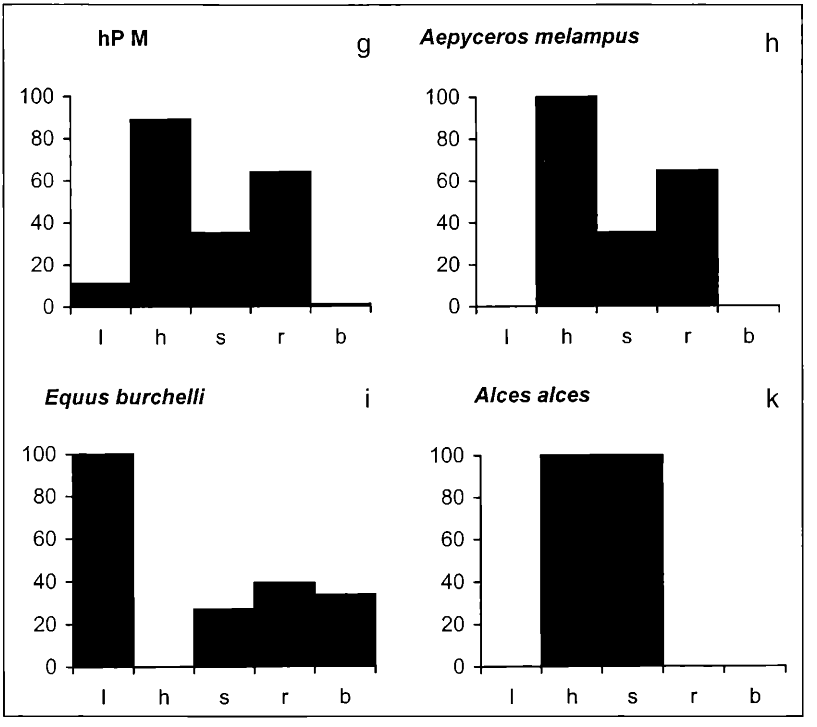


Figure 3. Histograms of mesowear features perlow, perhigh, persharp, perround and perblunt. Histograms are based on the summary values given in Table 2. a-e) experimental data of *Hippotherium primigenium*; f) consensus; g) mean; h-k) comparative histograms based on published data by FORTELIUS & SOLOUNIAS (in press); h) hypsodont mixed feeder *Aepyceros melampus* (impala); i) hypsodont grazer *Equus burchelli* (Burchell's zebra); k) brachydont browser *Alces alces* (moose).

nificant (P=0.090) if hP4 is omitted, indicating, that all data are close, but hP4 is more different from the others.

The cluster diagrams computed here show relations of datasets by positioning them in the same clusters. The closer the data are, the higher is the class of subclusters they share, and the smaller is the normalized Euclidian distance (NED) at the branching point of this cluster. The exact sequence and direction of species arrangement in the diagram however may not be interpreted as an expression of gradual (sequential) differences.

Cluster analysis using the index of hypsodonty and all mesowear variables polarise the full set of 60 recent and fossil species used as reference and the 7 experimental datasets (hP1-5, hPM, hPC) into a pattern with grazers and browsers at the extremes and with mixed feeders in between (Figures 4, 5). Grazers and browsers, although clearly clumped at one end also tend to occur interspersed with mixed feeders throughout the mixed feeder range. Mixed feeders also occur interspersed with the browsers. There are three main clusters, one containing mainly grazers, one containing the majority of mixed feeders, and one corresponding



to the attrition-dominated end of the spectrum containing most of the browsers and some of the attrition-dominated mixed feeders.

All species included (Figure 4a)
When datasets hP1-hP5, hPM (mean) and hPC (consensus) are treated as different species, cluster analysis of the mesowear characters perhigh, persharp, perround classify all experimental datasets of *Hippotherium primigenium* with mixed feeders. The cluster of NED 6, formed by hP3 and hP2 is shared by the extant bovid *Tetracerus quadricornis* (Tq), the chousingha. In the same cluster hierarchy hP1 and hP5 cluster with *Tragelaphus angasi* (Ta), the nyala and *Aepyceros melampus* (Me), the impala, *Camelus dromedarius* (Cl), the dromedary, a common fossil bovid *Pachytragus crassicornis* (cR) and the fossil equid *Merychippus insignis* (ml) (Figure 4a, 5a). Datasets hP1, hP2, hP3 and hP5 are within the same subcluster of NED 10. HP4 shares the subcluster NED 18 with the remaining experimental data. Among others, hP4 shares a cluster of NED 15 with the bovids *Ovis canadensis* (Oc), the bighorn sheep, *Gazella granti* (Gg), the Grant's gazelle, *Tragelaphus scriptus* (Ts), the bushbuck and *Taurotragus oryx* (To), the eland. With the exception of the browsing bovid *Boocercus euryceros* (BE), the bongo, all are mixed feeders classifying hP4 still in the central part of the attrition/abrasion spectrum. Dataset hPM is classified in the same cluster of NED 2 as hP2 and hP3, while hPC shares a cluster with hP1 and hP5.

Typical and fossil species (Figure 4b)
In this case, there are three main clusters, one for true grazers, one for less extreme grazers and mixed feeders, and one for mixed feeders and browsers. The cluster shared by mixed feeders and browsers is clearly divided into two subclusters, with most of the mixed feeders forming one subcluster, and the browsers forming the other.
The grazer-mixed feeder cluster classifies all datasets of *H. primigenium* together with the hypsodont mixed-feeder *Aepyceros melampus* (Me; impala) and the hypsodont grazers *Connochaetes taurinus* (ct; wildebeest), *Hippotragus niger* (hn; sable antelope) and *Kobus elipsiprymnus* (ke; waterbuck). All experimental datasets of *H. primigenium* hP1-hP5, hPC and hPM are classified in the same subcluster of NED 20, together with the impala, the extinct equids *Merychippus insignis* (ml) and *Cormohipparion quinni* (cQ) and the extinct bovid *Pachytragus crassiciornis* (cR).

Index of hypsodonty excluded (Figure 5a, b)
When mesowear variables perhigh, persharp and perround are used for classification without the index of hypsodonty, no differences are seen in hierarchical

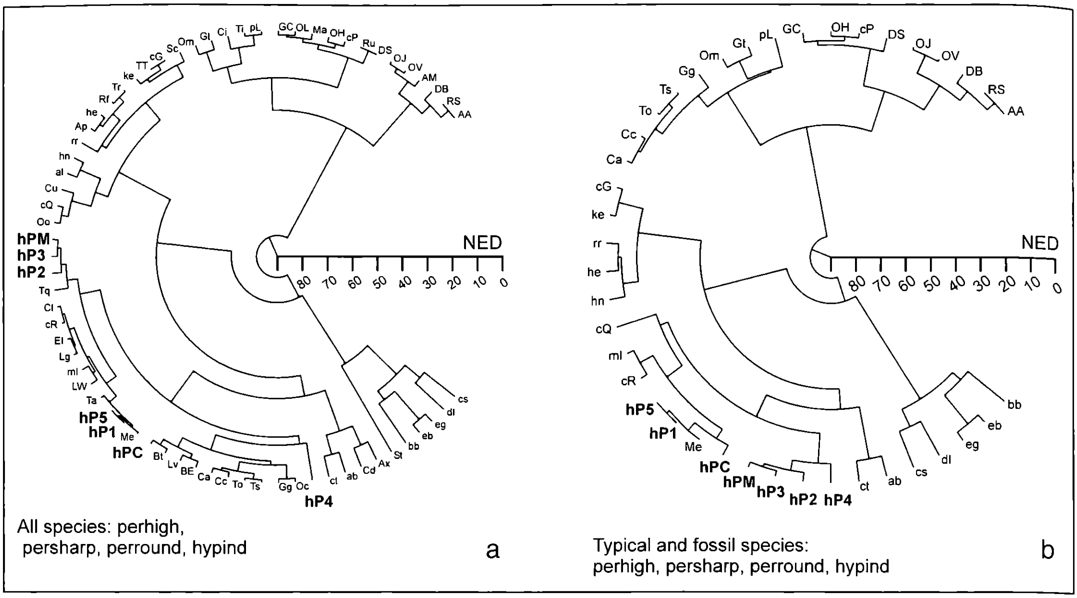


Figure 4. Hierarchical cluster diagrams based on the mesowear features percent high occlusal relief, percent sharp cusps and percent round cusps and the index of hypsodonty from JANIS (1988). a) Clusters based on all recent and fossil species included in this study; b) Clusters based on a set of "typical" recent and fossil species after FORTELIUS & SOLOUNIAS (in press). Symbols as in Table 4, UPPER CASE = BROWSER, lower case = grazer, Mixed case (Capital first) = Mixed-feeder, mixed Case (lower First) = fossil species. Bold = datasets of *Hippotherium primigenium*. NED = normalized euklidian distance.

classification of clusters and in linkage patterns of clusters. All species are classified in the homologous clusters. Only minor differences in the NED measures of cluster branches occur in comparison to the classification based on perhigh, persharp, perround and hypind.

Discussion

The dietary adaptation of *Hippotherium primigenium*

Cluster analysis of the data results in a number of observations. Comparing all species, the two subclusters contain all experimental data and 13 recent species which are mixed feeders with three exceptions. These exceptions are the brachydont browsers *Ammodorcas clarkei* (El), *Litocranius walleri* (LW), and *Boocercus euryceros* (BE). The consensus dataset is consistently next to the hypsodont mixed-feeder *Aepyceros melampus* (impala), no matter if the index of hypsodonty is included (Figures 4a, b) or excluded (Figures 5a, b), or if all comparative species are classified (Figures 4a, 5a), or only the "typical" (Figures 4b, 5b). When only typical and fossil species are compared, all datasets are classified in the abrasion – dominated mixed feeder range. As a consensus diagnosis, a mixed diet with grassy components similar to the diet of the impala (*Aepyceros melampus*) is thus suggested. *Hippotherium primigenium* is also close to the fossil equid *Merychippus insignis* (ml), the microwear signal of which suggests a significant proportion of abrasive elements (grass) in it's diet (HAYEK et al. 1992). Thus, a mixed feeder dietary category is the most likely interpretation for both *Hippotherium primigenium* from the Vallesian Dinotheriensande and *Merychippus insignis* from the Miocene of Nebraska. The fact that *M. insignis* is a mixed feeder is of intrinsic interest because *M. insignis* is the sister-taxon of the most primitive hipparion, *Cormohipparion goorisi*. These two taxa are further known to have been sympatric in their geographic and chronologic range (WOODBURNE et al. 1996). HAYEK et al. (1992) demonstrated using tooth microwear analysis that *Cormohipparion goorisi* was a grazer and clearly distinguished from the tooth microwear of *Merychippus insignis* in its dietary adaptation. The fact that *Hippotherium primigenium* is a mixed feeder is also interesting as it supports the emerging evidence that Central European *Hippotherium primigenium* periodically utilised browse (the essence of a mixed feeder), from subtropical forested environments (BERNOR et al. 1988). Although we have not studied the entire group, the same may have been the case for the ancestors of *H. primigenium* after their immigration into Europe nearly 11 million years ago. The mixed feeder interpretation is not just supported by

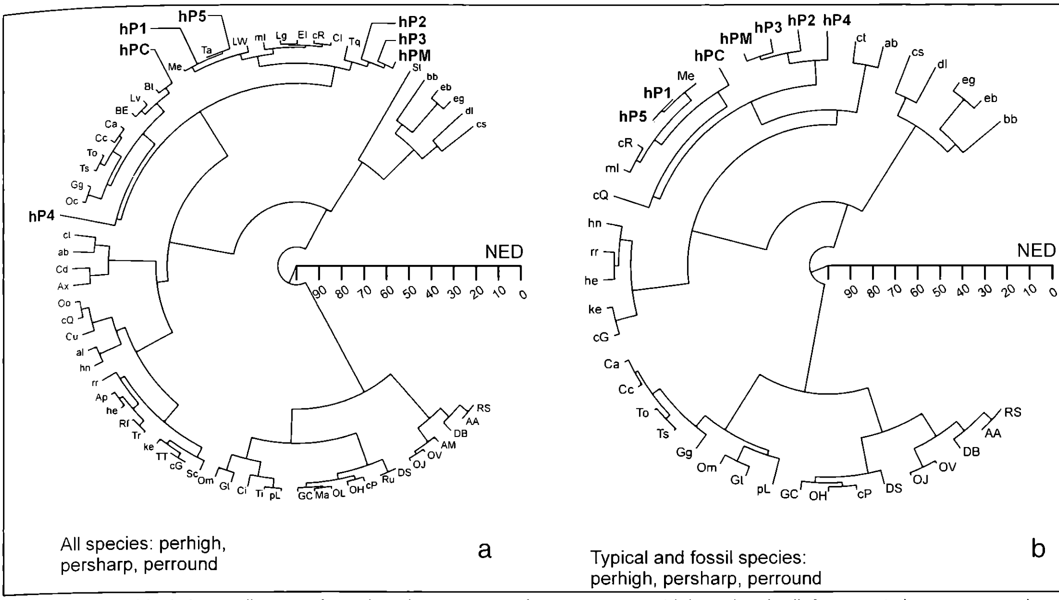


Figure 5. Hierarchical cluster diagrams based on the mesowear features percent high occlusal relief, percent sharp cusps and percent round cusps. a) Clusters based on all recent and fossil species included in this study; b) Clusters based on a set of "typical" recent and fossil species after FORTELIUS & SOLOUNIAS (in press). Symbols as in Table 4, UPPER CASE = BROWSER, lower case = grazer, Mixed case (Capital first) = Mixed-feeder, mixed Case (lower First) = fossil species. Bold = datasets of *Hippotherium primigenium*. NED = normalized euklidian distance.

studies of dental microwear and mesowear, but facial and postcranial anatomy and independent paleoecological studies based on plants (BERNOR et al. 1988, KOVAR-EDER et al. 1996).

Robustness of the Mesowear Method

We have tested the mesowear method by comparing the individual scoring frequencies of the mesowear variables (perhigh, perlow, persharp, perround and perblunt). Testing the cusp shape variables, we find no significant differences between the datasets hP1-hP5. Comparing the histograms we find high degrees of similarity in the occlusal relief data (perhigh, perlow) in hP1-hP5. General trends such as the prevalence of perhigh versus perlow, the prevalence of round cusps and the underrepresentation of blunt cusps are consistent in all individuals and in the consensus and mean datasets. If the three broad dietary categories used by FORTELIUS & SOLOUNIAS are applied, comparison of the individual histograms with the data provided by FORTELIUS & SOLOUNIAS show highest degrees of correspondence with species in the mixed feeder category. This diagnosis would apply for all individual datasets hP1-hP5 as well as for the consensus and the mean dataset. We furthermore notice that cluster analysis places all individual datasets within the spectrum of mixed feeders, indicating that each individual dataset would have yielded the same paleodietary signal for *Hippotherium primigenium*. It is of particular interest to note that hP4, which is the only dataset fairly different in the occlusal relief variables, is still classified within the mixed feeder spectrum (Figures 4, 5). This observation gives strong evidence that the mesowear method is robust, and resistant to variation in individual scoring practice.

However, we have noticed that hP4 is isolated from the rest of the dataset at the level of subcluster 6. Although still consistently placed within the mixed feeders, hP4 is clearly deviant and therefore a critical dataset for evaluating the robusticity of the method. Inspection of the raw data reveals obvious differences in the scoring frequency of the mesowear character occlusal relief (Figure 3d). The scoring "low" occurs much more frequently in dataset hp4, a fact that probably explains the shift towards the abrasion dominated edge of the spectrum.

The effect of hypsodonty on the pattern is negligible: virtually the same tree is obtained whether hypsodonty is included (Fig. 4a, b) or excluded (Fig. 5a, b), a result also reported by FORTELIUS & SOLOUNIAS (in press). However, hypsodonty has been shown to be the single most powerful variable for classifying species according to their dietary regime, yielding a higher percentage of correctly classified species than any (other) mesowear variable alone (FORTELIUS & SOLOUNIAS, in press). The fact that adding hypsodonty has no significant effect on the pattern can be interpreted as strong evidence for the power of the mesowear signal in its most basic form.

The differences in scoring frequencies, although insignificant for the dietary reconstruction in this contribution, does point to difficulties in defining cut-off points in the mesowear scoring protocol. We therefore emphasise that the calibration of mesowear variables is one of the crucial tasks to be done in order to make the mesowear method a universal, comprehensive and thoroughly robust method for paleodietary reconstruction in ungulates.

Acknowledgements

We sincerely thank all museums for access to specimens. Hessisches Landesmuseum (Darmstadt), Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt), American Museum of Natural History (New York), National Museum of Natural History (Washington D. C.), Natural History Museum (London), and the Royal Museum of Central Africa (Tervuren, Belgium). The study was supported in part by NSF IBN 9628263 to SOLOUNIAS.

Literature

ANDREWS, P A. & BERNOR, R. L. (1999): Vicariance Biogeography and Paleoecology of Eurasian Miocene hominoid Primates. – In: AUGUSTI, J., ROOK, L. & ANDREWS, P. (Eds.): The Evolution of Neogene Terrestrial Ecosystems in Europe: 454-488; Cambridge (Cambridge University Press).

BERNOR, R. L. & ARMOUR-CHELU, M. (1999): Towards an Evolutionary History of African Hipparionine Horses – In: BROMAGE, T. & SCHRENK, F. (Eds.): African Biogeography, Climate Change and Early Hominid Evolution, Wenner-Gren Foundation Conference, Livingstonia Beach Hotel, Salima, Malawi: 189-215; Oxford (Oxford).

BERNOR, R. L., KAISER, T M., KORDOS, L. & SCOTT, R. S. (1999): Stratigraphic Context, Systematic Position and Paleoecology of *Hippotherium sumegense* KRETZOI, 1984 from MN 10 (Late Vallesian of the Pannonian Basin). – Mitteilung der Bayerischen Staatssammlung für Paläontologie und historische Geologie, **39**: 1-35.

BERNOR, R. L., KOVAR-EDER, J., Lipscomb, D., Rögl, F. Sen, S. & Tobien, H. (1988): Systematics, stratigraphic and paleoenvironmental contexts of first-appearing Hipparion in the Vienna Basin, Austria. – Journal of Vertebrate Paleontology, **8**: 427-452. Vienna.

BERNOR, R. L., TOBIEN, H., HAYEK, L.-A. & MITTMANN, H.-W. (1997): *Hippotherium primigenium* (Equidae, Mammalia) from the late Miocene of Höwenegg (Hegau, Germany). – Andrias, **10**: 1- 230.

BERNOR, R. L., TOBIEN, H. & WOODBURNE, M. O. (1989): Patterns of Old World hipparionine evolutionary diversification and biogeographic extension. – In: LINDSAY, E. H., FAHLBUSCH, V. & MEIN, P. (Eds.): Topics on European Mammalian Chronology: 263-319; New York (Plenum).

EISENMANN, V., ALBERDI, M.-T DE GIULI, C. & STAESCHE, U. (1988): Studying Fossil Horses – In: WOODBURNE, M. O. & SONDAAR, P Y (Eds.): Collected papers after the "New York International Hipparion Conference, 1981", Volume I: Methodology: 1-71; Leiden (Brill).

EISENMANN, V. & SONDAAR, P (1998): Pliocene vertebrate locality of Calta, Anakara, Turkey. 7 Hipparion. – Geodiversitas, **20** (3): 409-440.

FORTELIUS, M. & SOLOUNIAS, N. (in press). Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. – American Museum Novitates.

HAYEK, L.-A., BERNOR, R. L., SOLOUNIAS, N. & STEIGERWALD, P. (1992): Preliminary studies of Hipparionine horse diet as measured by tooth microwear. – Ann. Zool. Fennici, **28**: 187-200.

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: RUSSEL, D. E. SANTORIO, J. P & SIGNOGNEU-RUSSEL, D. (Eds.): Teeth Revisited. Proceedings of the VII International Symposium on Dental Morphology. – Muséum national d'Histoire Naturelle, Memoire série C, **53**: 367-387; Paris (Museum National d'Histoire Naturelle Press).

JANIS, C. M. (1995): Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. – In: THOMASON, J. J. (Ed.): Functional morphology in vertebrate paleontology: 76-97; Cambridge (University Press).

KOVAR-EDER, J., KVACEK, Z., ZASTAWNIAK, E., GIVULESU, R., HABLY, L., MIHAJLOVIC, D., TESLENKO, J. & WALTHER, H. (1996): Floristic trends in the vegetation of the Paratethys surrounding areas during Neogene time. – In: BERNOR, R. L., FAHLBUSCH, V. & MITTMANN, H.-W. (Eds.): The Evolution of Western Eurasian Neogene Mammal Faunas: 395-413; New York (Columbia University Press).

MACFADDEN, B. J., CERLING, T E. & PRADO, J., (1996): Cenozoic terrestrial ecosystem evolution in Argentinia: Evidence from carbon isotopes of fossil mammal teeth. – Palaios, **5** (11): 319-327

MACFADDEN, B. J., SOLOUNIAS, N. & CERLING, T.E. (1999): Ancient diets, ecology, and extinctions of 5-million-year-old horses from Florida. – Science, **283**: 824-827

SOLOUNIAS, N. & DAWSON-SAUNDERS, B. (1988): Dietary adaptations and paleoecology of the late Miocene ruminants from Pikermi and Samos in Greece. – Paleogoegraphy, Paleoclimatology, Paleoecology, **65**: 149-172.

SOLOUNIAS, N. & HAYEK, L-A. C. (1993): New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. – J. Zool., London **229**: 421-445.

SOLOUNIAS, N. & MOELLEKEN, S. C. M. (1993): Dietary adaptations of some extinct ruminants as determined by the premaxillary shape. – J. Mammalogy, **74**: 1059-1074.

STEININGER, F. F., BERGGREN, W. A., KENT, D. V., BERNOR, R. L., SEN, S. & AGUSTI, J. (1996): Circum-Mediterranean Neogene (Miocene and Pliocene) Marine-Continental Chronologic Correlations of European Mammal Units. – In: BERNOR, R. L., FAHLBUSCH, V & MITTMANN, H.-W. (Eds.): The Evolution of Western Eurasian Neogene Mammal Faunas: 7-46; New York (Columbia University Press).

TEAFORD, M. F. (1988): A review of dental microwear and diet in modern mammals. – Scanning Microscopy, **2**: 1149-1166.

WOODBURNE, M. O., BERNOR, R. L. & SWISHER III, C. C. (1996): An appraisal of the stratigraphic and phylogenetic bases for the "Hipparion Datum" in the Old World. – In: BERNOR, R. L., FAHLBUSCH, V. & MITTMANN, H.-W. (Eds.): The Evolution of Western Eurasian Neogene Mammal Faunas: 124-136; New York (Columbia University Press).