Extending the tooth mesowear method to extinct and extant equids

Thomas M. KAISER
Zoological Institute and Museum, University Greifswald,
J. S. Bach Str. 11-12, D-17489 Greifswald (Germany)
Kaiser@mail.uni-greifswald.de

Nikos SOLOUNIAS
Department of Anatomy, New York College of Osteopathic Medicine
of the New York Institute of Technology, Old Westbury, NY 11568 8000 (USA)
nsolouni@iris.nyit.edu

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ABSTRACT

A new approach of reconstructing ungulate diets, the mesowear method, was introduced by Fortelius & Solounias (2000). Mesowear is based on facet development on the occlusal surfaces of the teeth. Restricting mesowear investigation on the M2 as has previously been suggested would limit application of the mesowear methodology to large ungulate assemblages. Most of the fossil, subfossil and recent ungulate assemblages that have been assigned to a single taxon have a smaller number of individuals. This results in the demand to extend the mesowear method to further tooth positions in order to obtain stable dietary classifications of fossil taxa. The focus of this paper is to test, if a consistent mesowear classification is obtainable for the remaining positions of the upper cheek tooth dentition (P2, P3, P4, M1 and M3) and for combinations of these tooth positions. For statistical testing, large assemblages of isolated cheek teeth of the Vallesian hipparionine horse *Hippotherium primigenium* Meyer, 1829 and of two populations of the recent zebra *Equus burchelli* Gray, 1824 are employed as models. Subsequently, all single cheek tooth positions and all possible combinations of these tooth positions are tested for their consistency in classification of the mesowear variables compared to the M2, the model tooth of Fortelius & Solounias (2000). As the most consistent model for the proposed "extended" mesowear method, the combination of four tooth positions P4, M1, M2, and M3 is identified, which allows to include the largest number of isolated tooth specimens from a given assemblage, and fulfills the demand of being consistent in the dietary mesowear classification with the "original" mesowear method. We propose the "extended" mesowear method to be particularly well suited for the reconstruction of paleodiets in hypsodont equids.

KEY WORDS
Equidae,
Hippotherium,
Equus burchelli,
mesowear method,
methodology,
paleodiet,
paleobiology,
paleoenvironment.

RÉSUMÉ

L'application de la méthode d'usure des dents (« mesowear ») aux équidés fossiles et actuels.

Une nouvelle approche pour reconstruire le régime des ongulés a été proposée récemment par Fortelius & Solounias (2000) : la méthode du « mesowear ». Cette approche est fondée sur le développement des surfaces occlusales des dents. La restriction à l'utilisation d'une seule dent, la M2, comme il a été suggéré initialement, nécessite un échantillonnage d'une certaine importance en terme d'individus, ce qui réduit l'application de la méthode à un nombre limité d'ensembles fossilifères. En effet un taxon fossile, subfossile, ou même récent, présente rarement un nombre suffisant de spécimens pour en satisfaire les conditions optimales d'utilisation. D'où le besoin d'élargir la méthode aux autres dents de la rangée supérieure pour la rendre plus performante. L'objectif de cet article est de tester la cohérence de la méthode du mesowear avec les autres dents de la rangée supérieure (P2, P3, P4, M1 et M3), isolées ou en combinaisons différentes. La riche collection de dents jugales de l'équidé Vallesien *Hippotherium primigenium* Meyer, 1829 et celles de deux populations du zèbre récent *Equus burchelli* Gray, 1824 ont été utilisées pour tester l'approche à l'aide des méthodes statistiques. Ensuite, toutes les dents isolées et leurs combinaisons possibles ont été testées pour prouver la cohérence avec la méthode classique de Fortelius & Solounias (2000). Comme résultat de l'application de la méthode, quatre dents deviennent donc utilisables : P4, M1, M2 et M3 ; ce qui permet de considérer un plus grand nombre de spécimens par taxon dans le même ensemble fossile, sans perdre de cohérence avec l'approche classique. Nous concluons que la « méthode élargie du mesowear » est particulièrement bien adaptée pour la reconstitution des paléorégimes des équidés hypsodontes.

MOTS CLÉS
Equidae,
Hippotherium,
Equus burchelli,
méthode de mesowear,
méthodologie,
paléorégime,
paléobiologie,
paléoenvironnement.

INTRODUCTION

Reconstructing the dietary adaptation of fossil ungulates provides important information on the adaptation of individual species and ultimately on habitat conditions of terrestrial mammalian paleocommunities. Previous attempts have been undertaken using a variety of methods, which include stable isotope signatures (e.g., MacFadden *et al.* 1996, 1999) and tooth microwear analysis (Hayek *et al.* 1992; Solounias & Hayek 1993; Solounias & Moelleken 1993a; Solounias & Semprebon 2002). Teaford (1988) and Janis (1995) have reviewed microwear research. In addition, tooth crown height analysis (Janis 1988), and various masticatory morphology analyses (Solounias & Moelleken 1993b; Solounias & Dawson-Saunders 1987; Eisenmann 1998) have also been used to interpret paleodiets. The two tooth microwear methods (scanning microscopy and light microscopy) have proven to be relatively laborious. The masticatory methods are usually based on a very small sample size. The original mesowear method covered large samples but examined only one apex per individual. The present study extends the mesowear to all apices and examines statistically varying results due to combinations of various tooth positions. As a result four tooth positions (P4, M1, M2, and M3) are identified as ideal for the interpretation of fossil specimens allowing to include the largest number of isolated tooth specimens from a given assemblage. These four positions are the model of the "extended" mesowear method.

THE ORIGINAL MESOWEAR METHOD

A new approach for reconstructing ungulate diet, the mesowear method, was introduced by Fortelius & Solounias (2000). Mesowear is based on facet development on the occlusal surfaces of the ungulate upper molar 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 that mesowear analysis focused on the buccal cutting edges of the enamel surfaces where the buccal wall (ectoloph) meets the occlusal plane. There, mesowear was simply defined by two variables: 1) as cusp relief (high or low); and 2) as cusp shape (sharp, rounded, or blunt) in buccal (lateral) view. These simple expressions of tooth wear were found to have strong dietary diagnostic capabilities for ungulate diets.

In collecting the data the 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 is classified as high (h) or low (l), depending on how high the cusps rise above the valley between them. The second mesowear variable, cusp shape, includes three scored attributes: sharp (s), round (r) and blunt (b) according to the degree of facet development (Fig. 1). 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. For each species the respective cusp shapes were summarized as percentages and are given in Table 1 as the three variables %sharp, %round and %blunt. The one apex of a single tooth mesowear method was tested and applied to hipparionine horses by Bernor *et al.* (in press), Kaiser (in press), Kaiser *et al.* (2000a, b, in press).

HIPPARIONINE HORSES AS A MODEL

Hipparionine horses are tridactyl and usually with well developed preorbital fossae and isolated protocones. They are ideal for the application of mesowear methods because they are abundant, they include many species, and species often have extensive geographic and chronological ranges. Moreover, the species are morphologically diverse and recent analyses of their cranial, dental and postcranial anatomy has shown, that they were adapted to a broad range of habitats and feeding adaptations (Bernor *et al.* 1990; Bernor & Armour-Chelu 1999; Eisenmann & Sondaar 1998).

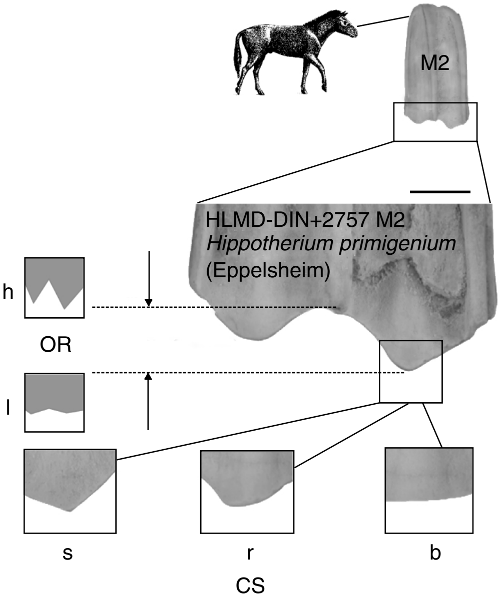


FIG. 1. — The mesowear variables of an hypsodont ungulate cheek tooth (as defined by Fortelius & Solounias 2000). The occlusal relief (**OR**) may be scored “high” (**h**) or “low” (**l**), the cusp shape (**CS**) is classified as “sharp” (**s**), “round” (**r**) and “blunt” (**b**). Reconstruction of *Hippotherium primigenium* Meyer, 1829 after O. Garreaux (*in* Bernor *et al.* 1997). Scale bar: 5mm.

ABBREVIATIONS

AMNH	American Museum of Natural History, New York;
HLMD	Hessisches Landesmuseum, Darmstadt;
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main;
LSNK	Landessammlungen für Naturkunde, Karlsruhe;
LMM	Landesmuseum, Mainz;
Di	Dinotheriensande (all localities);
Ep	Eppelsheim;
Es	Esselborn;
We	Westhofen;
m.a.	million years ago (Mega anum);

OR	occlusal relief;
CS	cusp shape;
$RP_{(om)}$	reference position of the "original" mesowear method (after Fortelius & Solounias 2000);
$RP_{(em)}$	reference position of the "extended" mesowear method (as defined in this study).

ISSUES IN DEVELOPING THE MESOWEAR DATA AND MODEL

The "original" mesowear method used only one apex per individual (the sharpest apex of the M2; Fortelius & Solounias 2000). The larger the number of tooth apices (positions) for each individual specimen included in a study the more reliable the representation of the diet eaten and hence of the paleodietary investigation. The focus of the present study is to test, if a consistent mesowear classification is obtainable for all apices in the dentition of the hipparionine species *Hippotherium primigenium* Meyer, 1829 and for two populations of modern *Equus burchelli* Gray, 1824, one northern (ebN) and one southern (ebS). The following conditions have to be fulfilled by a model tooth position:

– 1) an isolated tooth, as is the case in many fossil assemblages, needs to be identified as to which tooth it is. In hypsodont equids identification of isolated teeth is possible for all marginal (P2-P3 and M2-M3) by means of the distinctly developed anterior or posterior tilts of these teeth (Fig. 2). In P4 and M1 however identification is difficult because the tooth tilts are only poorly and inconsistently developed. These tooth positions therefore are hard to identify with certainty, if the specimens are isolated;

– 2) a model tooth position should emphasize the center of the tooth battery. The anterior and posterior margins of the tooth row participate less in food processing. A reduced amount of vegetation to be chewed at the margins may result in a more pronounced attrition (tooth to tooth contact);

– 3) the masseter and pterygoid musculature are located posteriorly. Consequently, chewing pressures should vary along the tooth row, with higher pressures in the molars and lower pressures in the premolars.

These conditions collectively imply that the most ideal teeth for a model of chewing should be P3 and M2. P3 comes into occlusion before M2 (Joubert 1972) and therefore its wear stage should be more advanced than that of M2. Consequently, in any attritional assemblage of fossil individuals representing all age classes, upper second molars should therefore be more likely in early to medium wear than P3s. As a single model tooth, the M2 therefore actually appears the best-suited single tooth position.

Isolated teeth predominate in many fossil equid taphocoenoses. In addition, a single individual is frequently represented by only one tooth specimen in a given fossil assemblage (e.g., Behrensmeyer 1975; Kaiser 1997; Kaiser *et al.* 1995; Prindiville 1998). The larger the number of tooth positions available for reconstructing paleodiet, the larger the basis for statistical analysis, making dietary reconstruction more significant. According to Fortelius & Solounias (2000), a mesowear pattern becomes stable when at least 20 specimens are sampled. A large number of tooth positions incorporated into a model further on allows the incorporation of more individuals in a mesowear study than a single tooth model.

The hipparionine assemblage of the Dinotheriensande (Germany, Vallesian, MN9) is one of the largest in Europe. However, in such a large assemblage, only 22 M2 specimens are known (Fig. 4). A number just large enough to allow a statistically meaningful mesowear classification. Restricting the mesowear investigation to the M2, as the single model tooth, would only allow comparisons to assemblages of comparable size and therefore would restrict mesowear analysis to only very few additional assemblages. An additional complication is that most of the other fossil assemblages and recent species in collections have lower numbers of individuals than those of the Dinotheriensande. Consequently, it is necessary to extend the original model of the mesowear method to additional tooth positions in order to obtain the most reliable dietary classifications of fossil taxa.

The focus of this paper is therefore to test, if a consistent mesowear classification is obtainable

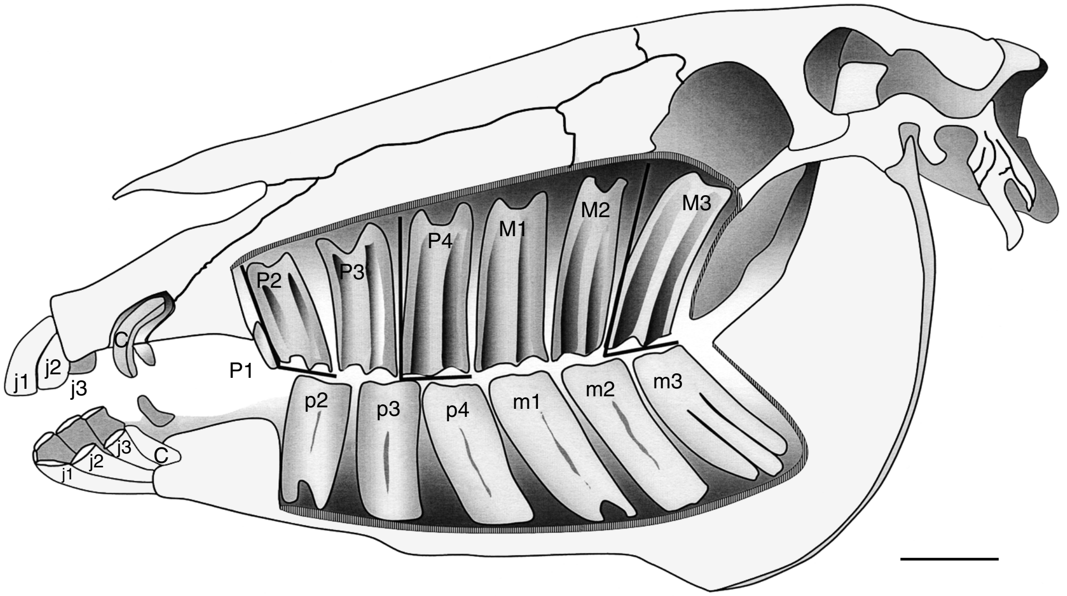


FIG. 2. — Longitudinal section of the scull of a six year old individual of *Equus ferus* Boddaert, 1785 (after Butz & Böttger 1946). The tooth alveolae are opened. Note the differences in tilt of the individual cheek tooth positions as indicated by lines. In the upper premolars P2 and P3 the angle between the occlusal surface and the anterior wall of the tooth is open, in the upper P4 and M1 it is about rectangular, and in the upper molars M2 and M3 the occlusal surface forms a close angle with the anterior wall (bold lines). P2 and P3, as well as M2 and M3 are therefore easily to be identified if isolated. P4 and M1 however are to be distinguished with a great degree of uncertainty. The same applies to the lower premolars and molars. Scale bar: 5 cm.

for the remaining tooth positions (P2, P3, P4, M1 and M3) and for various combinations of these tooth positions. We therefore identify a combination of tooth positions as a new reference model for a proposed "extended" mesowear method, which provides a mesowear classification consistent with the "original" mesowear method by Fortelius & Solounias (2000). This reference model has to meet the following conditions:

– 1) to provide a large number of data; as many cheek tooth positions (apices) as possible. We plan to maximize the number of tooth positions into the model;

– 2) as a means of consistency with the "original" mesowear method, the same variables are to be used.

MATERIAL

Two samples of recent zebras and one fossil Miocene assemblage were used. One of the extant samples consisted of 32 individuals of *Equus burchelli* treated as 182 tooth specimens (ebN, Appendix A; from the AMNH and the SMF). All specimens belonged to wild shot animals collected from different localities from Sudan, Kenya and Tanzania. The sample contained 27 P2s, 30 P3s, 31 P4s, 33 M1s, 33 M2s and 28 M3s (Fig. 5E). The second extant sample (ebS, Appendix B) consisted of 23 wild shot individuals of *Equus burchelli* from Botswana, Namibia and Angola. The sample consisted of 117 specimens; 20 P2s, 20 P3s, 19 P4s, 21 M1s, 20 M2s and 17 M3s (Fig. 5F).

As a fossil reference sample, a large number of isolated cheek teeth of *Hippotherium primigenium* from the upper Miocene (Vallesian, MN9) is one of the largest in Europe (Dinotheriensande, Rheinhessen, Germany; Appendix C). The chronological homogeneity of the Dinotheriensande sample, which includes several localities (Fig. 3), is uncertain, but using tooth morphology, there is no reason to believe that more than one species is present in this sample. The Dinotheriensande localities are all placed within the

TABLE 1. — Frequency of mesowear variables in the recent comparison taxa (data from Fortelius & Solounias 2000), and the fossil populations of Vallesian (MN9) *Hippotherium primigenium* Meyer, 1829 and recent *Equus burchelli* Gray, 1824 (ebN and ebS) investigated in this study. Abbreviations: **low**, percent low occlusal relief; **high**, percent high occlusal relief; **sharp**, percent sharp cusps; **round**, percent round cusps; **blunt**, percent blunt cusps; code 1: **m**, "mabra group" after Fortelius & Solounias (2000); **n**, neutral species; **t**, species with typical dietary adaptation; **r**, reference samples investigated; code 2: classification of dietary preferences according to the conservative classification by Fortelius & Solounias (2000); **G**, grazer; **M**, mixed feeder; **B**, browser; **f**, fossil taxon.

Taxon	Author	Abbrev.	Low (%)	High (%)	Sharp (%)	Round (%)	Blunt (%)	Code 1	Code 2
Alces alces	Linnaeus, 1758	AA	0,0	100,0	100,0	0,0	0,0	t	B
Ammodorcas clarkei	Thomas, 1891	EI	0,0	100,0	28,5	71,4	0,0	n	B
Antilocapra americana	Ord, 1815	AM	4,0	96,0	88,6	11,3	0,0	n	B
Boocercus euryceros	Ogilby, 1837	BE	0,0	100,0	44,4	55,5	0,0	n	B
Capreolus capreolus	Linnaeus, 1758	OL	4,0	96,0	72,0	25,0	2,9	n	B
Cephalophus dorsalis	Gray, 1846	DR	7,0	93,0	32,1	60,7	7,1	m	B
Cephalophus natalensis	Smith, 1834	NA	0,0	100,0	16,6	83,3	0,0	m	B
Cephalophus niger	Gray, 1846	NI	9,0	91,0	35,4	61,2	3,2	m	B
Cephalophus nigrifrons	Gray, 1871	NG	18,0	82,0	25,0	70,4	4,5	m	B
Cephalophus silvicultor	Afzelius, 1815	SL	20,0	80,0	0,0	94,8	5,1	m	B
Dendrohyrax arboreus	Smith, 1827	DA	0,0	100,0	50,0	50,0	0,0	m	B
Dendrohyrax dorsalis	Fraser, 1855	DD	18,0	82,0	46,4	53,5	0,0	m	B
Dicerorhinus sumatrensis	Fisher, 1814	DS	0,0	100,0	80,0	20,0	0,0	t	B
Diceros bicornis	Linnaeus, 1758	DB	0,0	100,0	94,1	5,8	0,0	t	B
Giraffa camelopardalis	Linnaeus, 1758	GC	6,0	94,0	73,7	26,2	0,0	t	B
Heterohyrax brucei	Gray, 1868	HB	64,0	36,0	81,8	18,1	0,0	m	B
Hyaemoschus aquaticus	Ogilby, 1841	HY	0,0	100,0	16,6	83,3	0,0	m	B
Litocranius walleri	Brooke, 1879	LW	4,0	96,0	33,3	66,6	0,0	n	B
Odocoileus hemionus	Rafinesque, 1817	OH	0,0	100,0	72,7	27,2	0,0	t	B
Odocoileus virginianus	Zimmermann, 1780	OV	0,0	100,0	88,8	11,1	0,0	t	B
Okapia johnstoni	Sclater, 1901	OJ	0,0	100,0	87,5	12,5	0,0	t	B
Rhinoceros sondaicus	Desmarest, 1822	RS	0,0	100,0	100,0	0,0	0,0	t	B
Tragelaphus strepsiceros	Pallas, 1766	TT	0,0	100,0	0,0	100,0	0,0	n	B
Alcelaphus buselaphus	Pallas, 1766	ab	43,0	57,0	3,2	66,6	28,0	t	G
Alcelaphus lichtensteinii	Lichtenstein, 1812	al	18,0	82,0	5,8	82,3	11,7	n	G
Bison bison	Linnaeus, 1758	bb	100,0	0,0	0,0	26,6	73,3	t	G
Ceratotherium simum	Burchell, 1817	cs	100,0	0,0	0,0	72,0	28,0	t	G
Connochaetes taurinus	Lichtenstein, 1812	ct	45,0	55,0	15,3	55,7	28,8	t	G
Damaliscus lunatus	Burchell, 1823	dl	80,0	20,0	20,0	60,0	20,0	t	G
Equus burchelli	Gray, 1824	eb	100,0	0,0	27,0	39,3	33,6	t	G
Equus grevyi	Oustalet, 1882	eg	100,0	0,0	34,4	41,3	24,1	t	G
Hippotragus equinus	Desmarest, 1804	he	15,0	85,0	3,8	96,1	0,0	t	G
Hippotragus niger	Harris, 1838	hn	15,0	85,0	0,0	85,0	15,0	t	G
Kobus ellipsiprymnus	Ogilby, 1833	ke	4,0	96,0	0,0	100,0	0,0	t	G
Redunca redunca	Pallas, 1767	rr	9,0	91,0	6,4	90,9	2,5	t	G
Aepyceros melampus	Lichtenstein, 1812	Me	0,0	100,0	35,2	64,7	0,0	t	M
Antidorcas marsupialis	Zimmermann, 1780	Ma	4,0	96,0	73,0	26,9	0,0	n	M
Axis axis	Erxleben, 1777	Ax	21,0	79,0	6,9	67,4	25,5	n	M
Axis porcinus	Zimmermann, 1780	Ap	12,0	88,0	4,1	95,8	0,0	n	M
Boselaphus tragocamelus	Pallas, 1766	Tr	13,0	87,0	0,0	100,0	0,0	n	M
Budorcas taxicolor	Hodgson, 1850	Bt	5,0	95,0	42,1	57,8	0,0	n	M
Camelus dromedarius	Linnaeus, 1758	Cl	0,0	100,0	31,2	68,7	0,0	n	M
Capra ibex	Linnaeus, 1758	Ci	3,0	97,0	54,1	37,5	8,3	n	M
Carpicornis sumatraensis	Bechstein, 1799	Ca	0,0	100,0	45,4	50,0	4,5	t	M
Cervus canadensis	Linnaeus, 1758	Cc	0,0	100,0	47,3	52,6	0,0	t	M
Cervus duvauceli	Cuvier, 1823	Cd	33,0	67,0	12,0	64,0	24,0	n	M
Cervus unicolor	Kerr, 1792	Cu	9,0	91,0	14,2	80,9	4,7	n	M
Gazella granti	Brooke, 1872	Gg	12,0	88,0	50,0	50,0	0,0	t	M
Gazella thomsoni	Gunther, 1884	Gt	12,0	88,0	55,4	43,1	1,3	t	M
Lama glama	Linnaeus, 1758	Lg	0,0	100,0	28,1	68,7	3,1	n	M
Lama vicugna	Molina, 1782	Lv	0,0	100,0	41,6	58,3	0,0	n	M
Ourebia ourebi	Zimmermann, 1783	Oo	4,0	96,0	21,8	77,3	0,7	n	M

Taxon	Author	Abbrev.	Low (%)	High (%)	Sharp (%)	Round (%)	Blunt (%)	Code 1	Code 2
Ovibos moschatus	Zimmermann, 1780	Om	19,0	81,0	57,6	42,3	0,0	t	M
Ovis canadensis	Shaw, 1804	Oc	13,0	87,0	48,3	51,6	0,0	n	M
Procavia capensis	Pallas, 1766	Pc	54,0	46,0	62,5	37,5	0,0	m	M
Redunca fulvorufula	Afzelius, 1815	Rf	14,0	86,0	0,0	100,0	0,0	n	M
Rhinoceros unicornis	Linnaeus, 1758	Ru	0,0	100,0	80,0	20,0	0,0	n	M
Saiga tatarica	Linnaeus, 1766	St	60,0	40,0	60,0	40,0	0,0	n	M
Syncerus caffer	Sparrman, 1799	Sc	0,0	100,0	0,0	93,5	6,4	n	M
Taurotragus oryx	Pallas, 1766	To	0,0	100,0	50,0	50,0	0,0	t	M
Tetracerus quadricornis	Blainville, 1816	Tq	9,0	91,0	28,5	71,4	0,0	n	M
Tragelaphus angasi	Gray, 1849	Ta	0,0	100,0	35,0	65,0	0,0	n	M
Tragelaphus imberbis	Blyth, 1869	Ti	0,0	100,0	61,2	38,7	0,0	n	M
Tragelaphus scriptus	Pallas, 1766	Ts	0,0	100,0	51,0	48,9	0,0	t	M
Equus burchelli (north)	Gray, 1824	ebN	80,3	19,7	23,4	43,7	33,0	r	G
Equus burchelli (south)	Gray, 1824	ebS	93,5	6,5	19,5	44,2	36,4	r	G
Hippotherium primigenium (Dinotheriensande)	Meyer, 1829	hP-Di	1,8	98,2	17,4	82,6	0,0	r	f
Hippotherium primigenium (Eppelsheim)	Meyer, 1829	hP-Ep	3,6	96,4	16,3	83,7	0,0	r	f
Hippotherium primigenium (Esselborn)	Meyer, 1829	hP-Es	0,0	100,0	17,9	82,1	0,0	r	f
Hippotherium primigenium (Westhofen)	Meyer, 1829	hP-We	0,0	100,0	11,1	88,9	0,0	r	f

lower part of MN9, the age of which is believed to be about 10.5 m.a. (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. This attribute of the sample makes this fossil assemblage more suitable for tooth height measurements and age estimations of individuals from such measurements. In other samples, bone often covers the teeth making such measurements rare or impossible. Only upper cheek teeth are investigated in this analysis. The sample investigated comprises a total of n = 349 upper cheek tooth specimens assignable to *H. primigenium*. From the total of 349 tooth specimens there were 93 P2s, 73 P3s, 63 P4s, 52 M1s, 22 M2s and 50 M3s (Fig. 4). The most frequently preserved tooth position is the P2, the least frequent however is the M2.

In order to attain consistency with Fortelius & Solounias (2000), tooth specimens not yet in occlusion and specimens showing initial wear were excluded as well as specimens with a persisting crown height of less than 15 mm and specimens where the actual tooth type (tooth position) cannot be known. After excluding such teeth, 330 specimens were used (Fig. 5A).

METHODS

Mesowear variables (low, high, sharp, round and blunt) were scored for the two recent zebra samples (ebN and ebS) and 330 specimens from the Dinotheriensande (as in Fortelius & Solounias 2000). Relative frequencies (percentages) were calculated for each isolated tooth position and each of the 63 combinations of tooth positions possible with one to six cheek tooth positions (Fig. 5).

Fortelius & Solounias (2000) used the tooth microwear of 53 ungulates and the literature as a basis for developing the dietary categorization of the mesowear data base of 64 ungulate species. Among these were species with variously problematic diets (namely the water chevrotain, the duikers and the hyraxes), which were grouped together in the mesowear study as the "mabra" group of "minute abraded brachydont". These

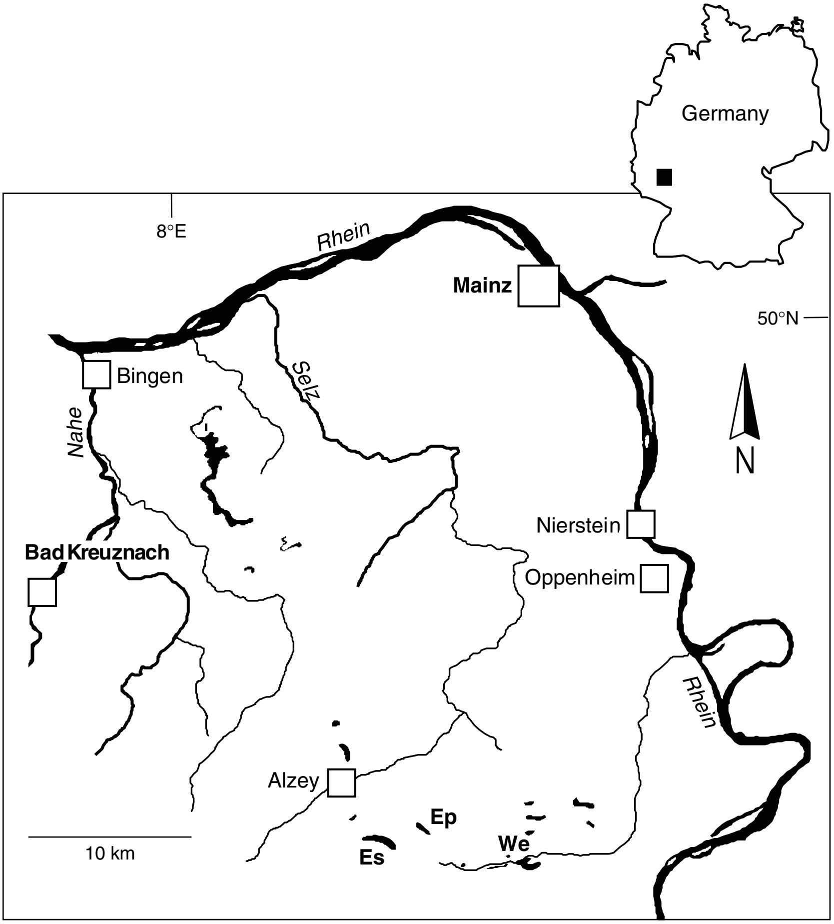


FIG. 3. — Geographic situation of the Vallesian (MN9) fossil localities of the Dinotheriensande (black signatures). The localities of Eppelsheim (**Ep**), Esselborn (**Es**) and Westhofen (**We**) are highlighted (after Franzen 1997 and Kaiser *et al.* in press).

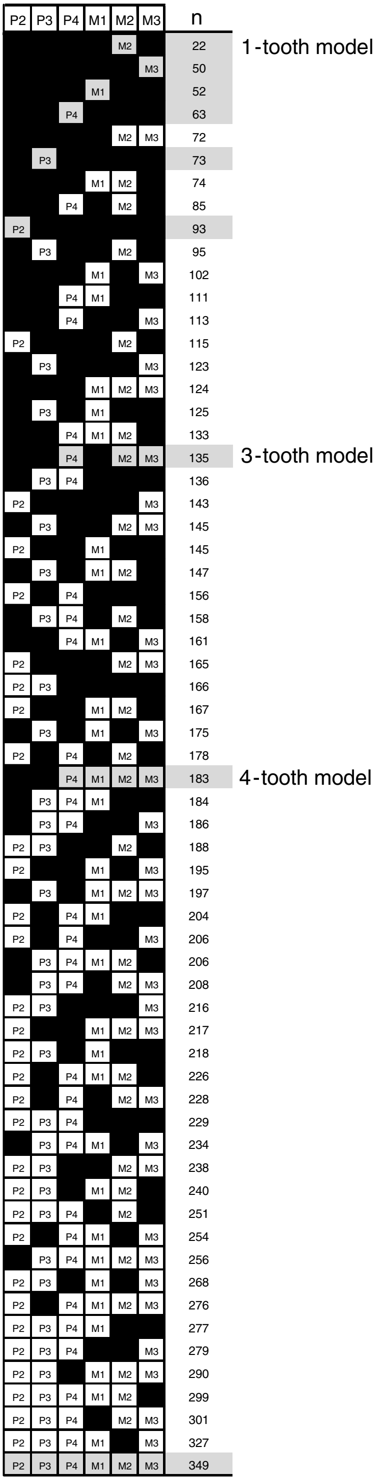
species were excluded in the present study. Analysis was undertaken using a reduced set of 27 "typical" recent species as a comparative set, which have been shown to provide reliable dietary data without complications in both mesowear and microwear analyses (Solounias & Semprebon 2002). Fortelius & Solounias (2000) found that for the 64 living species they investigated, the single variable that classified the species best was the index of hypsodonty (hypind) but the diagnostic resolution increased, as additional variables were included. We do not include the index of hypsodonty (from Janis 1988) into this study, because of its strong influence on the dietary classification it is expected to diminish the influence of the mesowear variables on the result of classification. Of the several dietary classifications Fortelius & Solounias (2000) tested, the conservative classification resulted in the most correct classification of species based on mesowear variables and the index of hypsodonty; more correct in terms of tooth microwear analysis (Solounias & Semprebon 2002). We presently follow the Fortelius & Solounias (2000) classification of extant species into the three broad dietary categories browser, mixed feeder and grazer. Molar and premolar crown height measurements were taken twice averaged and rounded to 0.1 mm using digital calipers. We refer to the conventions of Eisenmann *et al.* (1988) and Bernor *et al.* (1997).

STATISTICS

Chi-square "corresponding probabilities" (p) are computed between each of the 62 combinations of single and multiple tooth positions remaining and the M2 (Fig. 5) in order to test, if incorporating one or more tooth positions into the model has an influence on the mesowear classification. The resulting matrices are sorted in descending order after the p-value. The closer a single model is to the M2, the more similar is the distribution pattern of the mesowear variables. The M2, which is acting as the reference of this chi-square analysis has the p-value 1, while the p-values of all the other matrix columns are ≤ 1. The closer a column is to the p-value of 1, the higher is the probability, that the distribution of the mesowear variables of this model of tooth positions is not different from the reference position (M2). Hierarchical cluster analysis was further applied, with complete linkage (to enhance the distinctiveness of clusters), using the mesowear variables (%high, %sharp, %round and %blunt). For this analysis we use the original dataset of Fortelius & Solounias (2000) for the extant comparison species and the data presented in this study for *Equus burchelli* and *Hippotherium primigenium* (Table 1). All statistical tests were computed using Systat 9.0.

TESTING THE "EXTENDED" MODELS

The consistency in classification of the proposed "extended" model is tested using cluster analysis. The relative frequencies of mesowear variables



P2	P3	P4	M1	M2	M3	n	
				M2		22	1-tooth model
					M3	50	
			M1			52	
		P4				63	
				M2	M3	72	
	P3					73	
			M1	M2		74	
		P4		M2		85	
P2						93	
	P3			M2		95	
			M1		M3	102	
		P4	M1			111	
		P4			M3	113	
P2				M2		115	
	P3				M3	123	
			M1	M2	M3	124	
	P3		M1			125	
		P4	M1	M2		133	
		P4		M2	M3	135	3-tooth model
	P3	P4				136	
P2					M3	143	
	P3			M2	M3	145	
P2			M1			145	
	P3		M1	M2		147	
P2		P4				156	
	P3	P4		M2		158	
		P4	M1		M3	161	
P2				M2	M3	165	
P2	P3					166	
P2			M1	M2		167	
	P3		M1		M3	175	
P2		P4		M2		178	
		P4	M1	M2	M3	183	4-tooth model
	P3	P4	M1			184	
	P3	P4			M3	186	
P2	P3			M2		188	
P2			M1		M3	195	
	P3		M1	M2	M3	197	
P2		P4	M1			204	
P2		P4			M3	206	
	P3	P4	M1	M2		206	
	P3	P4		M2	M3	208	
P2	P3				M3	216	
P2			M1	M2	M3	217	
P2	P3		M1			218	
P2		P4	M1	M2		226	
P2		P4		M2	M3	228	
P2	P3	P4				229	
	P3	P4	M1		M3	234	
P2	P3			M2	M3	238	
P2	P3		M1	M2		240	
P2	P3	P4		M2		251	
P2		P4	M1		M3	254	
	P3	P4	M1	M2	M3	256	
P2	P3		M1		M3	268	
P2		P4	M1	M2	M3	276	
P2	P3	P4	M1			277	
P2	P3	P4			M3	279	
P2	P3		M1	M2	M3	290	
P2	P3	P4	M1	M2		299	
P2	P3	P4		M2	M3	301	
P2	P3	P4	M1		M3	327	
P2	P3	P4	M1	M2	M3	349	

FIG. 4. — Frequency of tooth specimens in the total assemblages of *Hippotherium primigenium* Meyer, 1829 known from the Dinotheriensande. Single tooth positions and combinations of tooth positions are sorted by number of specimens in descending order. Grey lines indicate all single tooth positions P2, P3, P4, M1, M2 and M3, the total of all positions of the cheek tooth row (P2-M3) and the combinations of tooth positions discussed as proposed models for the "extended" mesowear method in this contribution (1-tooth model (M2), 3-tooth model (P4+M2+M3) and 4-tooth model (P4-M3)). Abbreviation: **n**, number of specimens.

(%high, %sharp and %blunt) are computed for the reference combination of the proposed extended model (P4-M3), and for the M2, the reference position of the "original" mesowear method after Fortelius & Solounias (2000) and are plotted in a cluster analysis together with a set of extant reference taxa. As reference taxa the set of "typical" taxa and the classification of dietary adaptations in the extant comparison taxa follow Fortelius & Solounias (2002).

In addition to the total of all specimens of *H. primigenium* from all the Vallesian Dinotheriensande, these analyses are undertaken independently for the Dinotheriensande localities (Fig. 3) of Eppelsheim, Esselborn and Westhofen.

CHI-SQUARE RANKING MATRICES

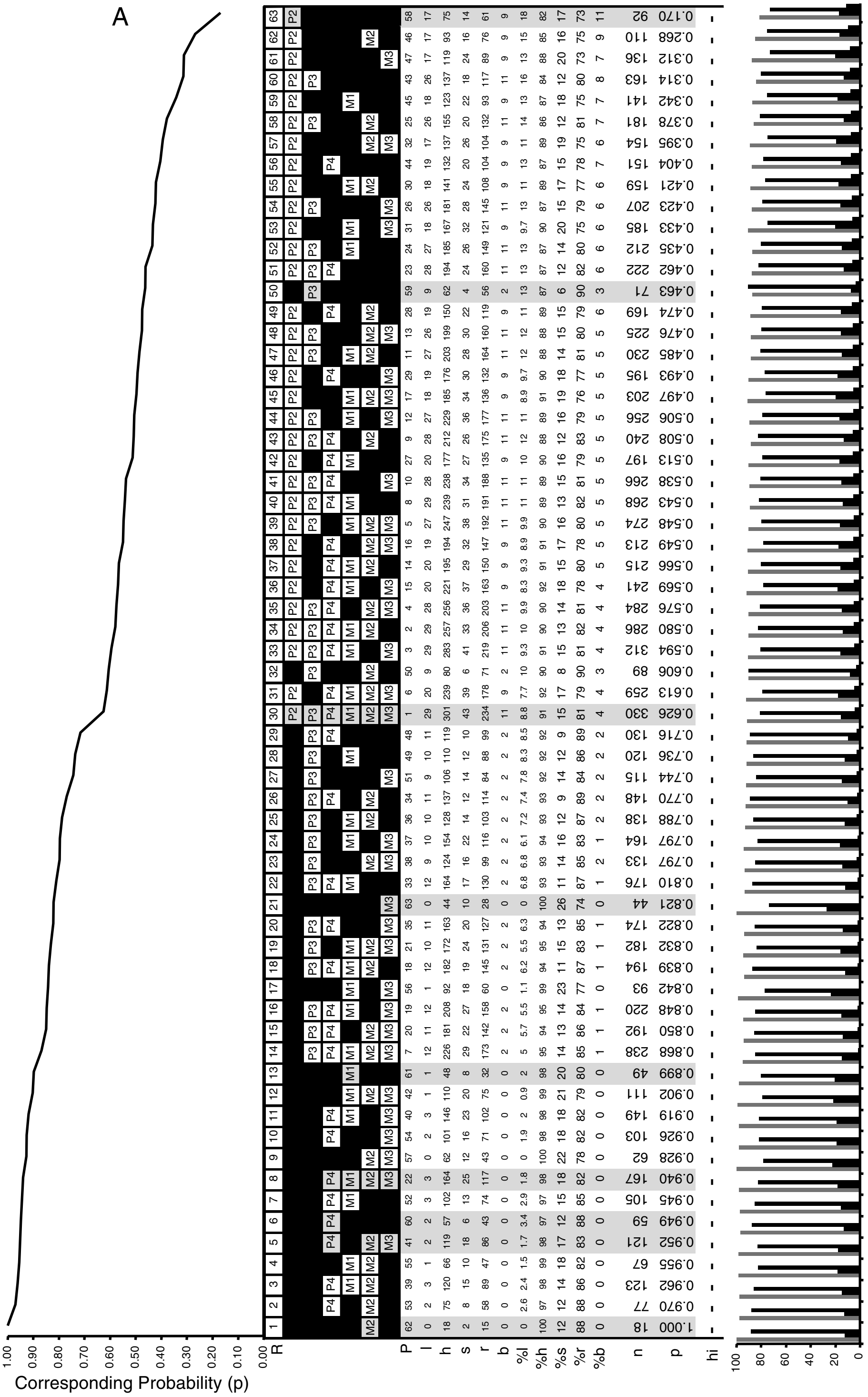
RESULTS OF CHI-SQUARE RANKING MATRICES

In the two recent zebra samples investigated, the corresponding probability (p) of the isolated tooth positions and of any combinations of tooth positions range between p = 1 for M2, the model position of Fortelius & Solounias (2000) and p < 0.001. The total of all tooth positions (P2+P3+P4+M1+M2+M3) has p-values of 0.009 for *E. burchelli* ebS (Fig. 5F) and 0.046 for *E. burchelli* ebN (Fig. 5E). This combination is therefore most likely different from the M2 data. Two combinations of 5-tooth positions are consistently classified in the range of corresponding probabilities indicating no difference in the classification from the M2 data. These are the combinations P3-M3 and P2+P4-M3. Only one combination of 4-tooth positions (P4+M1+M2+M3) is consistently within this range, and classifies better than the two 5-tooth models identified. One combination of 3-tooth positions (P4+M2+M3) classifies better than the 4-tooth model identified (P4+M1+M2+M3) in the two assemblages (Fig. 5E, F).

In *Hippotherium primigenium*, the corresponding probability (p) of all isolated tooth positions and of any combinations of tooth positions range between p = 1 for the M2, and p = 0.170 for the P2 for the Dinotheriensande assemblage as a whole (Fig. 5A). The total of all cheek tooth positions (P2-M3) ranges between 26 for Westhofen (Fig. 5D) and 33 for Eppelsheim (Fig. 5B) of 63 possible positions in the ranking of chi-square probabilities and thus occupies an intermediate position. The p-values for this combination range between 0.626 (Dinotheriensande, all localities, Fig. 5A) and 0.9 (Esselborn, Fig. 5C) and therefore are most likely not different from the M2. The only combination of 5-tooth positions consistently classifying better than the total of all positions is the 5-tooth model P3-M3, and only the combination of 4-tooth positions (4-tooth model) P4+M1+M2+M3 is consistently better classified than is the total of all cheek teeth. With the exception of M2, the "original" 1-tooth model, only one 3-tooth model (P4+M2+M3) is classified better than the 4-tooth model P4+M1+

▶

FIG. 5. — Chi-square ranking matrix of the absolute frequencies of mesowear variables "low" (**l**), "high" (**h**), "sharp" (**s**), "round" (**r**) and "blunt" (**b**) calculated for 63 single and multiple tooth positions. Wear stages incorporated exclude very early wear and specimens with less than 15 mm of crown height. Abbreviations: **R**, ranking position; **P**, number of combination of single and multiple tooth positions; **l**, **h**, **s**, **r**, **b**, absolute numbers of mesowear scores; **%l**, **%h**, **%s**, **%r**, **%b**, calibrated frequency (percentages) of mesowear variables; **n**, number of tooth specimens in a certain model; **p**, chi-square corresponding probability giving the probability, the null-hypotheses of independence should be rejected at an error probability of 0.05. The reference position for each test is the M2 (left column of the matrix, P = 62). The columns are sorted by decreasing p-values. Large p-value (left), small p-value (right). M2 (R = 1) always has the p-value of 1, because this position is the model position of the "original" mesowear method; **hi**, **-** (minus), null-hypotheses of independence should be rejected at an error probability of 0.05; the distribution patterns are likely to be equal; **+** (plus), null-hypotheses of independence cannot be rejected, the distribution patterns are likely to be different. Grey background: all single tooth positions P2, P3, P4, M1, M2 and M3, the total of all tooth positions (P2-M3) and the combination of tooth positions (4-tooth model) which is discussed as models for the proposed "extended" mesowear method. The bar charts to the bottom of each matrix plot indicate the calibrated frequencies (percentages) of mesowear variables for each column of the matrix. Gray, %h; black, %s, %r and %b. **A**-**D**, *Hippotherium primigenium* Meyer, 1829; **A**, from the Vallesian (MN9) Dinotheriensande (all localities); **B**, Eppelsheim; **C**, Esselborn; **D**, Westhofen; specimens housed at the HLMD, SMF, SNMK and LMM; **E**, Recent *Equus burchelli* Gray 1824 (sample ebN) from Sudan, Kenya and Tanzania; **F**, *Equus burchelli* (sample ebS) from Botswana, Namibia and Angola; specimens housed at the AMNH and the SMF.


A
Corresponding Probability (p)
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
R
P2
P3
P4
M1
M2
M3
P
l
h
s
r
b
%l
%h
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100
80
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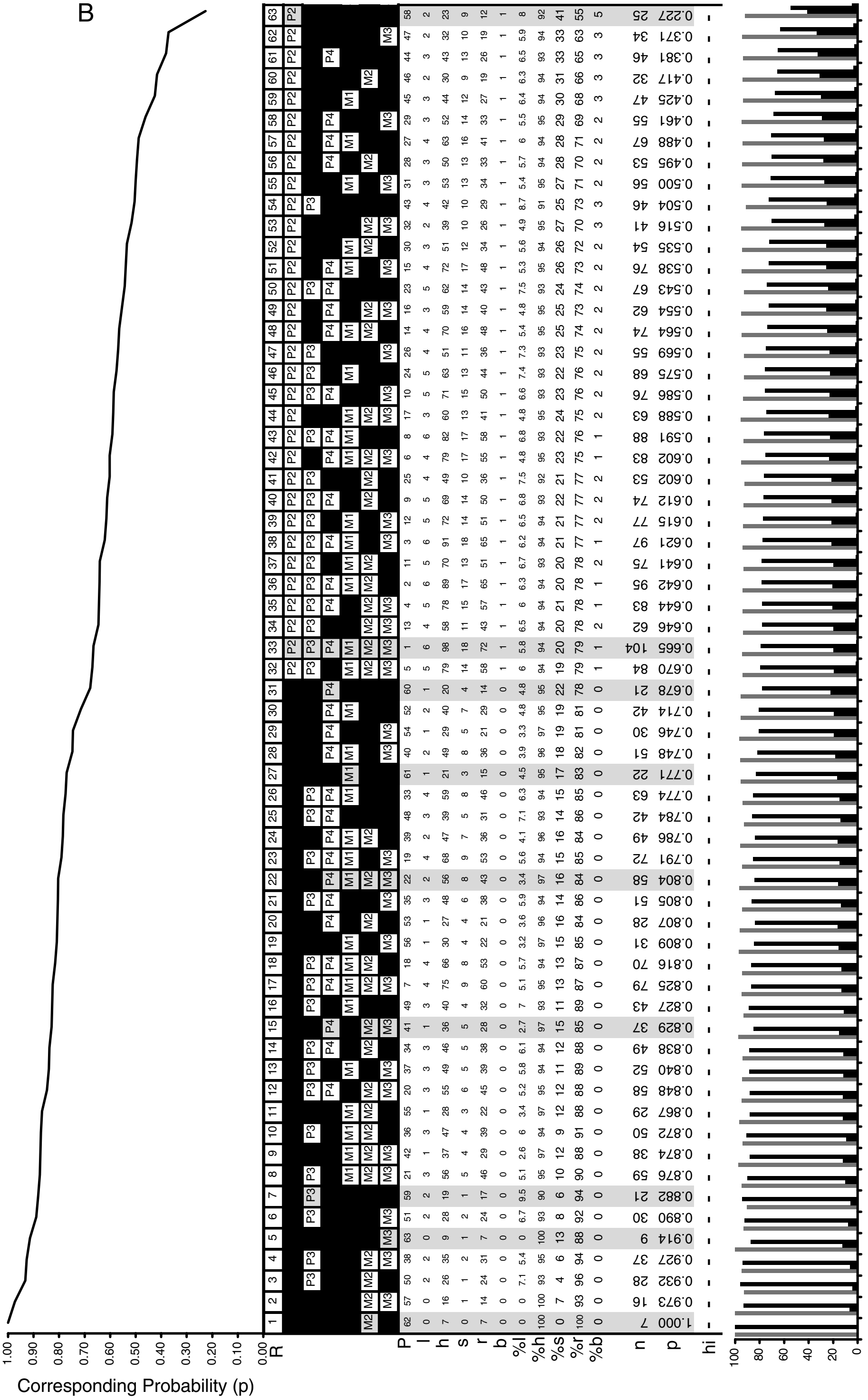
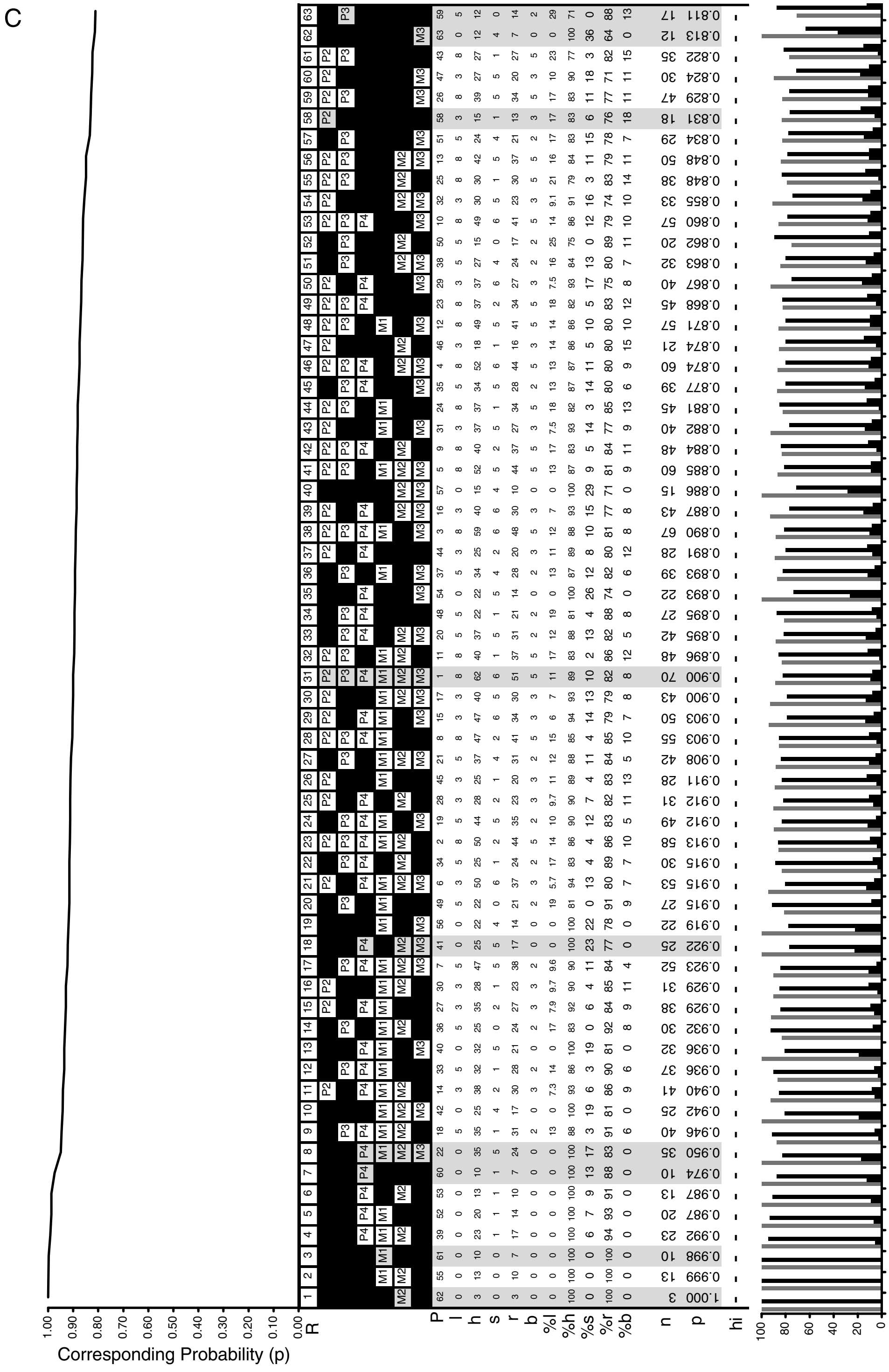


R							P	l	h	s	r	b	%l	%h	%s	%r	%b	n	p
1					M2		62	0	7	0	7	0	0	100	0	100	0	7	1.000
2					M2	M3	57	0	16	1	14	0	0	100	7	93	0	16	0.973
3		P3			M2		50	2	26	1	24	0	7.1	93	4	96	0	28	0.932
4		P3			M2	M3	38	2	35	2	31	0	5.4	95	6	94	0	37	0.927
5						M3	63	0	9	1	7	0	0	100	13	88	0	9	0.914
6		P3				M3	51	2	28	2	24	0	6.7	93	8	92	0	30	0.890
7		P3					59	2	19	1	17	0	9.5	90	6	94	0	21	0.882
8		P3		M1	M2	M3	21	3	56	5	46	0	5.1	95	10	90	0	59	0.876
9				M1	M2	M3	42	1	37	4	29	0	2.6	97	12	88	0	38	0.874
10		P3		M1	M2		36	3	47	4	39	0	6	94	9	91	0	50	0.872
11				M1	M2		55	1	28	3	22	0	3.4	97	12	88	0	29	0.867
12		P3	P4		M2	M3	20	3	55	6	45	0	5.2	95	12	88	0	58	0.848
13		P3		M1		M3	37	3	49	5	39	0	5.8	94	11	89	0	52	0.840
14		P3	P4		M2		34	3	46	5	38	0	6.1	94	12	88	0	49	0.838
15			P4		M2	M3	41	1	36	5	28	0	2.7	97	15	85	0	37	0.829
16		P3		M1			49	3	40	4	32	0	7	93	11	89	0	43	0.827
17		P3	P4	M1	M2	M3	7	4	75	9	60	0	5.1	95	13	87	0	79	0.825
18		P3	P4	M1	M2		18	4	66	8	53	0	5.7	94	13	87	0	70	0.816
19				M1		M3	56	1	30	4	22	0	3.2	97	15	85	0	31	0.809
20			P4		M2		53	1	27	4	21	0	3.6	96	16	84	0	28	0.807
21		P3	P4			M3	35	3	48	6	38	0	5.9	94	14	86	0	51	0.805
22			P4	M1	M2	M3	22	2	56	8	43	0	3.4	97	16	84	0	58	0.804
23		P3	P4	M1		M3	19	4	68	9	53	0	5.6	94	15	85	0	72	0.791
24			P4	M1	M2		39	2	47	7	36	0	4.1	96	16	84	0	49	0.786
25		P3	P4				48	3	39	5	31	0	7.1	93	14	86	0	42	0.784
26		P3	P4	M1			33	4	59	8	46	0	6.3	94	15	85	0	63	0.774
27				M1			61	1	21	3	15	0	4.5	95	17	83	0	22	0.771
28			P4	M1		M3	40	2	49	8	36	0	3.9	96	18	82	0	51	0.748
29			P4			M3	54	1	29	5	21	0	3.3	97	19	81	0	30	0.746
30			P4	M1			52	2	40	7	29	0	4.8	95	19	81	0	42	0.714
31			P4				60	1	20	4	14	0	4.8	95	22	78	0	21	0.678
32	P2	P3		M1	M2	M3	5	5	79	14	58	1	6	94	19	79	1	84	0.670
33	P2	P3	P4	M1	M2	M3	1	6	98	18	72	1	5.8	94	20	79	1	104	0.665
34	P2	P3			M2	M3	13	4	58	11	43	1	6.5	94	20	78	2	62	0.646
35	P2	P3	P4		M2	M3	4	5	78	15	57	1	6	94	21	78	1	83	0.644
36	P2	P3	P4	M1	M2		2	6	89	17	65	1	6.3	94	20	78	1	95	0.642
37	P2	P3		M1	M2		11	5	70	13	51	1	6.7	93	20	78	2	75	0.641
38	P2	P3	P4	M1		M3	3	6	91	18	65	1	6.2	94	21	77	1	97	0.621
39	P2	P3		M1		M3	12	5	72	14	51	1	6.5	94	21	77	2	77	0.615
40	P2	P3	P4		M2		9	5	69	14	50	1	6.8	93	22	77	2	74	0.612
41	P2	P3			M2		25	4	49	10	36	1	7.5	92	21	77	2	53	0.602
42	P2		P4	M1	M2	M3	6	4	79	17	55	1	4.8	95	23	75	1	83	0.602
43	P2	P3	P4	M1			8	6	82	17	58	1	6.8	93	22	76	1	88	0.591
44	P2			M1	M2	M3	17	3	60	13	41	1	4.8	95	24	75	2	63	0.588
45	P2	P3	P4			M3	10	5	71	15	50	1	6.6	93	23	76	2	76	0.586
46	P2	P3		M1			24	5	63	13	44	1	7.4	93	22	76	2	68	0.575
47	P2	P3				M3	26	4	51	11	36	1	7.3	93	23	75	2	55	0.569
48	P2		P4	M1	M2		14	4	70	16	48	1	5.4	95	25	74	2	74	0.564
49	P2		P4		M2	M3	16	3	59	14	40	1	4.8	95	25	73	2	62	0.554
50	P2	P3	P4				23	5	62	14	43	1	7.5	93	24	74	2	67	0.543
51	P2		P4	M1		M3	15	4	72	17	48	1	5.3	95	26	73	2	76	0.538
52	P2			M1	M2		30	3	51	12	34	1	5.6	94	26	72	2	54	0.535
53	P2				M2	M3	32	2	39	10	26	1	4.9	95	27	70	3	41	0.516
54	P2	P3					43	4	42	10	29	1	8.7	91	25	73	3	46	0.504
55	P2			M1		M3	31	3	53	13	34	1	5.4	95	27	71	2	56	0.500
56	P2		P4		M2		28	3	50	13	33	1	5.7	94	28	70	2	53	0.495
57	P2		P4	M1			27	4	63	16	41	1	6	94	28	71	2	67	0.488
58	P2		P4			M3	29	3	52	14	33	1	5.5	95	29	69	2	55	0.461
59	P2			M1			45	3	44	12	27	1	6.4	94	30	68	3	47	0.425
60	P2				M2		46	2	30	9	19	1	6.3	94	31	66	3	32	0.417
61	P2		P4				44	3	43	13	26	1	6.5	93	33	65	3	46	0.381
62	P2					M3	47	2	32	10	19	1	5.9	94	33	63	3	34	0.371
63	P2						58	2	23	9	12	1	8	92	41	55	5	25	0.227


C
Corresponding Probability (p)
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
R
P
l
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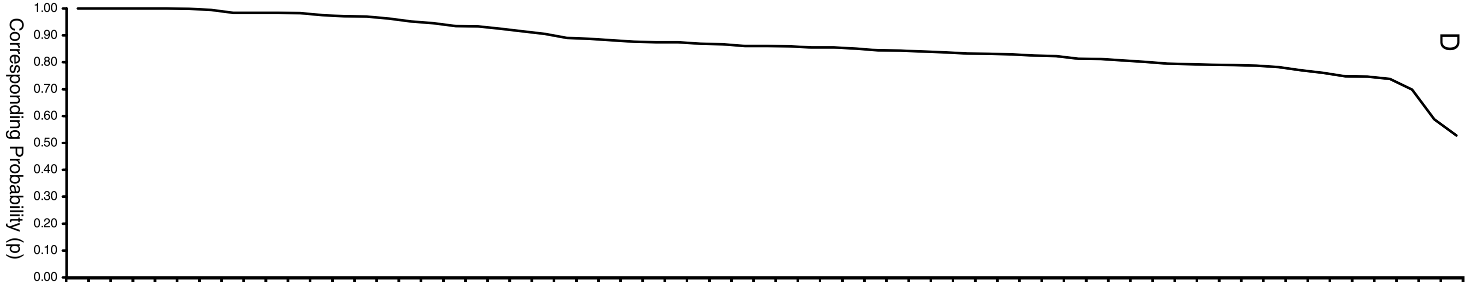
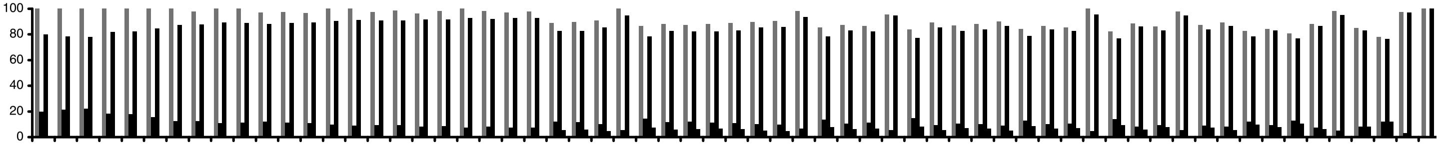
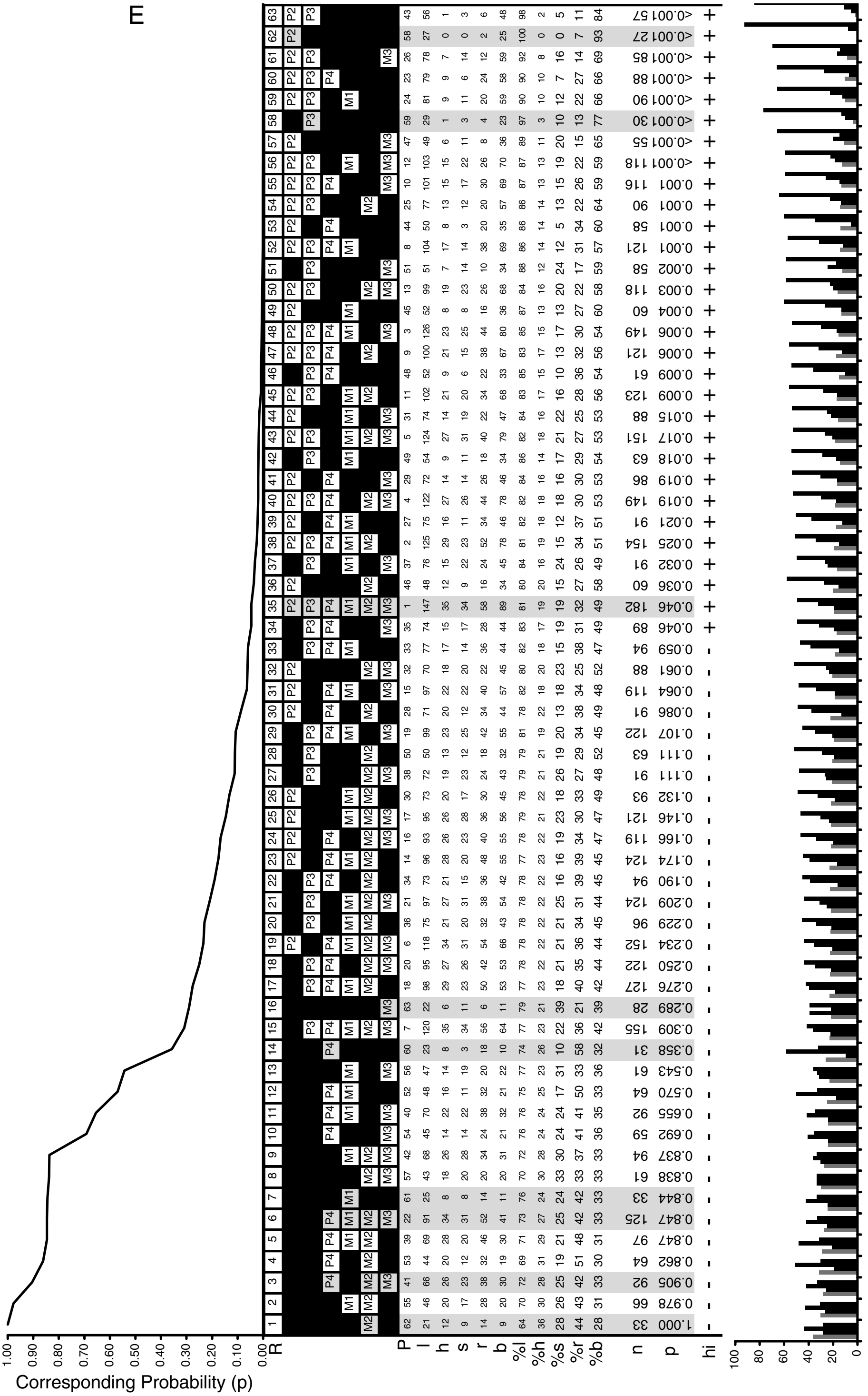


R	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
								P3			P3	P3	P3			P3	P3	P3	P3		P3
									P4	P4				P4	P4		P4		P4	P4	P4
				M1	M1	M1	M1	M1		M1		M1		M1		M1	M1			M1	M1
	M2	M2		M2		M2		M2	M2	M2	M2					M2	M2	M2	M2	M2	
		M3	M3	M3	M3			M3	M3	M3	M3	M3	M3	M3	M3		M3		M3		M3
P	62	57	63	42	56	55	61	21	41	22	38	37	51	40	54	36	7	50	20	39	19
l	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	1	1	1	0	1
h	5	14	9	24	19	15	10	44	31	41	34	39	29	36	26	35	61	25	51	32	56
s	1	3	2	4	3	2	1	5	3	4	4	4	3	3	2	3	5	2	4	2	4
r	4	11	7	18	14	11	7	36	25	32	29	32	25	28	21	29	50	22	43	25	46
b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
%l	0	0	0	0	0	0	0	2.2	0	0	2.9	2.5	3.3	0	0	2.8	1.6	3.8	1.9	0	1.8
%h	100	100	100	100	100	100	100	98	100	100	97	98	97	100	100	97	98	96	98	100	98
%s	20	21	22	18	18	15	13	12	11	11	12	11	11	10	9	9	9	8	9	7	8
%r	80	79	78	82	82	85	88	88	89	89	88	89	89	90	91	91	91	92	91	93	92
%b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
n	5	14	9	24	19	15	10	45	31	41	35	40	30	36	26	36	62	26	52	32	57
p	1.000	1.000	1.000	1.000	1.000	0.999	0.995	0.984	0.984	0.984	0.983	0.975	0.971	0.969	0.963	0.952	0.945	0.934	0.934	0.925	0.916
hi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

R	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
			P2	P2	P2		P2	P2	P2	P2	P2	P2	P2		P2	P2	P2		P2	P2	P2
	P3	P3	P3		P3			P3	P3			P3	P3	P3		P3	P3	P3		P3	
		P4		P4	P4	P4				P4	P4	P4	P4	P4						P4	P4
	M1		M1	M1	M1		M1	M1			M1		M1	M1	M1	M1					
			M2	M2	M2	M2	M2		M2	M2		M2		M2		M2			M2		
		M3	M3	M3	M3		M3	M3	M3	M3	M3	M3	M3		M3		M3		M3	M3	M3
P	49	35	5	6	1	53	17	12	13	16	15	4	3	18	31	11	26	59	32	10	29
l	1	1	9	8	9	0	8	9	9	8	8	9	9	1	8	9	9	1	8	9	8
h	30	46	72	69	89	22	52	67	62	59	64	79	84	52	47	63	57	20	42	74	54
s	2	3	9	8	9	1	8	8	8	7	7	8	8	3	7	7	7	1	7	7	6
r	25	39	62	58	76	18	44	58	55	51	54	69	72	43	40	55	51	18	37	65	47
b	0	0	4	4	4	0	4	4	4	4	4	4	4	0	4	4	4	0	4	4	4
%l	3.2	2.1	11	10	9.2	0	13	12	13	12	11	10	9.7	1.9	15	13	14	4.8	16	11	13
%h	97	98	89	90	91	100	87	88	87	88	89	90	90	98	85	88	86	95	84	89	87
%s	7	7	12	11	10	5	14	11	12	11	11	10	10	7	14	11	11	5	15	9	11
%r	93	93	83	83	85	95	79	83	82	82	83	85	86	93	78	83	82	95	77	86	82
%b	0	0	5	6	4	0	7	6	6	6	6	5	5	0	8	6	6	0	8	5	7
n	31	47	81	77	98	22	60	76	71	67	72	88	93	53	55	72	66	21	50	83	62
p	0.906	0.890	0.887	0.882	0.876	0.875	0.874	0.869	0.867	0.861	0.860	0.859	0.855	0.855	0.851	0.844	0.843	0.841	0.837	0.833	0.832
hi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

R	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
	P2	P2	P2	P2	P2		P2	P2	P2		P2	P2	P2	P2	P2	P2		P2	P2		
		P3		P3	P3			P3		P3		P3		P3		P3	P3			P3	
	P4	P4				P4		P4	P4	P4	P4	P4				P4	P4	P4		P4	P4
	M1	M1	M1	M1		M1					M1	M1	M1				M1				
	M2	M2	M2		M2			M2	M2	M2					M2						
							M3														
P	14	2	30	24	25	52	47	9	28	34	27	8	45	43	46	23	33	44	58	48	60
l	8	9	8	9	9	0	8	9	8	1	8	9	8	9	8	9	1	8	8	1	0
h	60	80	43	58	53	27	37	70	50	42	55	75	38	48	33	65	47	45	28	37	17
s	6	7	6	6	6	1	6	6	5	2	5	6	5	5	5	5	2	4	4	1	0
r	51	69	37	51	48	21	33	62	44	36	47	65	33	44	30	58	39	40	26	32	14
b	4	4	4	4	4	0	4	4	4	0	4	4	4	4	4	4	0	4	4	0	0
%l	12	10	16	13	15	0	18	11	14	2.3	13	11	17	16	20	12	2.1	15	22	2.6	0
%h	88	90	84	87	85	100	82	89	86	98	87	89	83	84	80	88	98	85	78	97	100
%s	10	9	13	10	10	5	14	8	9	5	9	8	12	9	13	7	5	8	12	3	0
%r	84	86	79	84	83	95	77	86	83	95	84	87	79	83	77	87	95	83	76	97	100
%b	7	5	9	7	7	0	9	6	8	0	7	5	10	8	10	6	0	8	12	0	0
n	68	89	51	67	62	27	45	79	58	43	63	84	46	57	41	74	48	53	36	38	17
p	0.830	0.825	0.822	0.813	0.812	0.807	0.802	0.795	0.793	0.791	0.790	0.788	0.782	0.770	0.761	0.748	0.747	0.738	0.699	0.588	0.528
hi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

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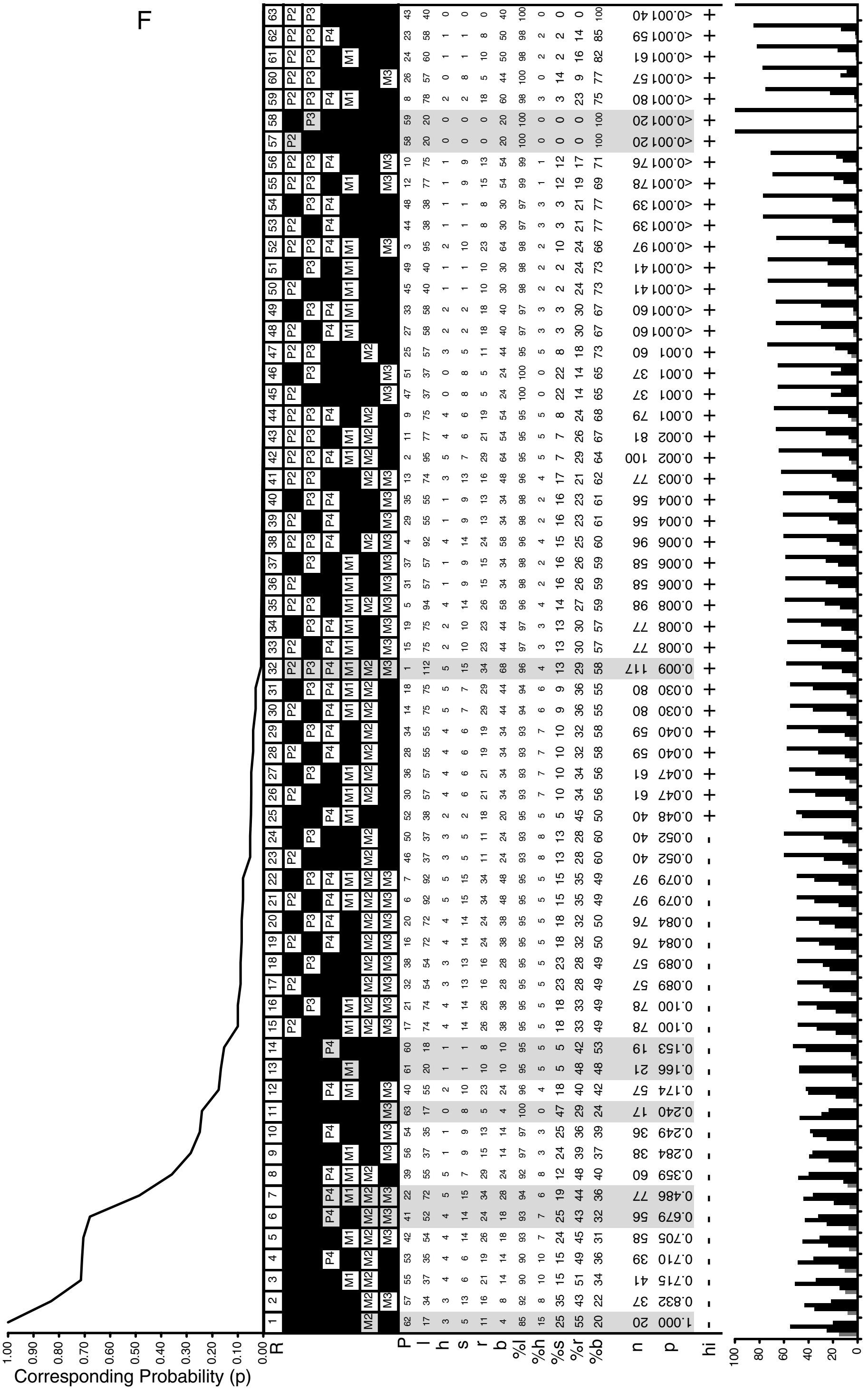
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Corresponding Probability (p)
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M2+M3 in all assemblages with the exception however of the Esselborn sample (Fig. 5C).

As concluding result we find, if P2 is disqualified, the resulting group of 5-tooth positions classifies better than the total of all tooth positions (P2-M3). The same applies in many samples, if the P3 is excluded, however this model mostly classifies in greater distance to the M2, than does the 5-tooth model P3-M3. The model consistently classifies within the range of p-values indicating no difference with the M2.

If the two first premolars of the cheek tooth row are excluded (remaining tooth positions = P4+ M1+M2+M3, the classification is closer to M2 than all remaining 5-tooth models. This is the closest model to that of the M2 (alone) model than the remaining 5-tooth models. In all samples such classification is within the range of p-values indicating no difference to the M2. This 4-tooth model is only succeeded in accuracy by the 3-tooth model P4+M2+M3. The 4-tooth model P4+M1+M2+M3 and the 3-tooth model (P4+M2+M3) are found to classify uniformly close to the M2 within the range of p-values indicating no statistically significant difference in mesowear classification with the reference position M2.

INTERPRETATION OF CHI-SQUARE COMBINATION MATRICES

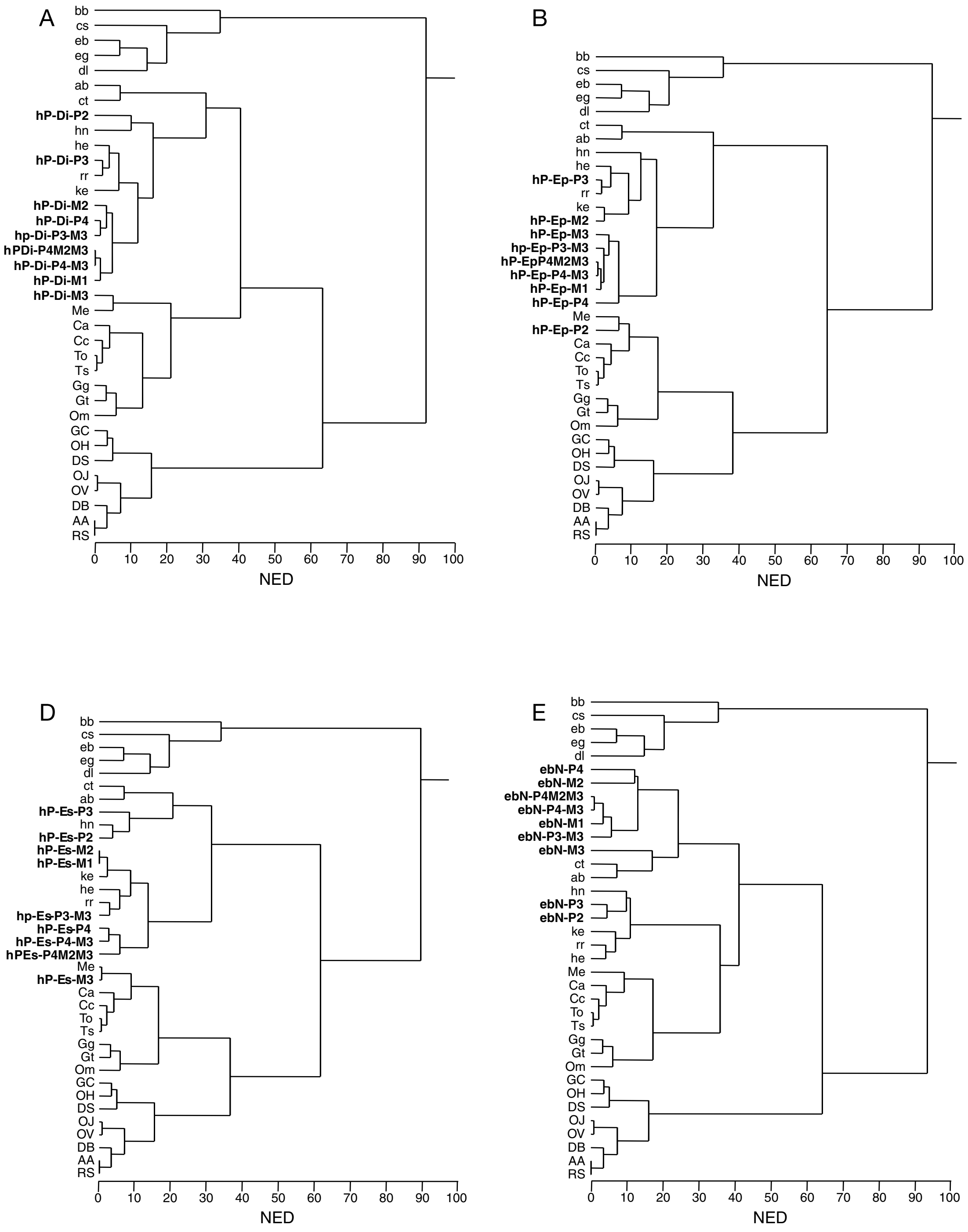
If all tooth positions were incorporated into the model, a maximum number of specimens would be available for investigation. The ranking position in the middle of the spectrum, the fact, that in the two *Equus burchelli* samples this model has p-values indicating the possibility of differences in the mesowear signature compared to the M2 ($RP_{(om)}$) as well as the observation, that P2 and P3 are the tooth positions correlating poorest in all assemblages investigated, are good arguments that these two tooth positions have an unfavorable influence on the consistency in classification with the "original" mesowear method. The fact that the 5-tooth model P3-M3, the 4-tooth model P4+M1+M2+M3 and the 3-tooth model P4+M2+M3 are within the range of p-values indicating similarity with the M2 ($RP_{(om)}$) and each consistently rules out any other models incorporating more tooth positions qualify each of these models for implementing a statistically sound "extended" mesowear methodology.

CLUSTER ANALYSIS

The following cluster analysis (Fig. 6) are meant to test how the mesowear datasets based on individual tooth positions (including the 1-tooth model of the "original" mesowear method, the M2, the 3-tooth model P4+M2+M3, the 4-tooth model P4-M3, and the 5-tooth model P3-M3 are classified within the field of 27 "typical" recent comparison taxa (Table 1). 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.

RESULTS OF CLUSTER ANALYSIS

In the samples of recent *Equus burchelli* the single tooth positions are classified within the spectrum of the grazers in both the ebS population (Fig. 6F), and the ebN population (Fig. 6E). In almost all of the fossil assemblages investigated, they are splinted in-between two of the basic dietary categories (Fig. 6A-D). In the Dinotheriensande localities investigated independently (Ep, Es, We), as well as in the total of *Hippotherium primigenium* specimens (Di), the P3 classifies within the "grazer" spectrum. This also applies for the P2 with the exception of the Eppelsheim sample (Fig. 6B), where the P2 is classified within the "mixed feeder" spectrum. Also the M3 classifies within the "mixed feeders" in the Di, and the Es samples (Fig. 6A, C). If the analysis were based on the M2 only (the model position of the original mesowear method) all individual samples from the Dinotheriensande, with the exception of the Westhofen sample would be classified as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hp-Di-P3-M3
hPDi-P4M2M3
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grazers, with a certain amount of browse in their diet. This is due to the proximity of the classifications to *Kobus ellipsiprymnus* Ogilby, 1833 (ke), *Hippotragus niger* Harris, 1838 (hn) and *Redunca redunca* Pallas, 1767 (rr) and also to the "mixed feeder" *Aepyceros melampus* Lichtenstein, 1812 (Me).

In all recent and fossil samples investigated, the 4-tooth model and the 3-tooth model are statistically very near. This also applies for tests of the 5-tooth model with the exception of the ebS sample of *E. burchelli*, where the 5-tooth model is classified in a different major cluster than the remaining models tested (Fig. 6F). 4- and 3-tooth model share a subcluster of little distance with the M2 ($RP_{(om)}$) and those recent species, that would also be the reference species for the M2 taken alone, the model position of the original mesowear method. With the exception of the Westhofen sample in all assemblages, the 3-tooth model and the 4-tooth model tested would classify within the same dietary category which also would be indicated by the M2 alone (Fig. 6).

INTERPRETATION OF CLUSTER ANALYSIS

The observed inconsistency in classification of isolated tooth positions in *Hippotherium primigenium* suggests the following implications:

– 1) based on the conservative dietary classification (after Fortelius & Solounias 2000) the mesowear signal of *H. primigenium* is close to the transition between "mixed-feeders" and "grazers". Consequently, the results of this taxon are sensitive regarding small differences in dietary determina-

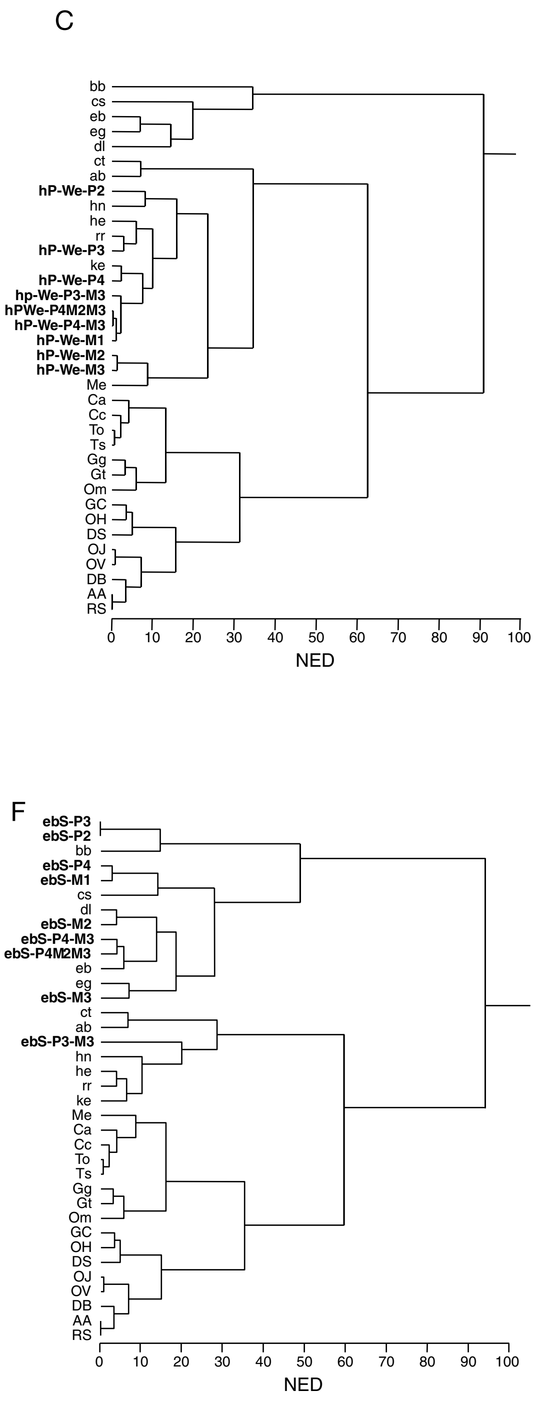

FIG. 6. — Hierarchical cluster diagrams based on the mesowear variables %high (percent high occlusal relief), %sharp (percent sharp cusps) and %blunt (percent blunt cusps) of the isolated tooth positions P2, P3, P4, M1, M2 and M3, the 3-tooth model P4+M2+M3, the 4-tooth model P4-M3 and the 5-tooth model P3-M3. Clusters based on a set of 27 "typical" recent comparison taxa after Fortelius & Solounias (2000); **A**-**D**, *Hippotherium primigenium* Meyer, 1829; **A**, from the Dinotheriensande (all localities); **B**, Eppelsheim; **C**, Esselborn; **D**, Westhofen; **E**, *Equus burchelli* Gray 1824 (ebN) from Sudan, Kenya and Tanzania; **F**, *Equus burchelli* (ebS) from Botswana, Namibia and Angola. For abbreviations see Table 1; **upper case**, browser; **lower case**, grazer; **mixed case (capital first)**, mixed-feeder; **mixed case (lower first)**, fossil species; **NED**, normalised Euclidean distance.

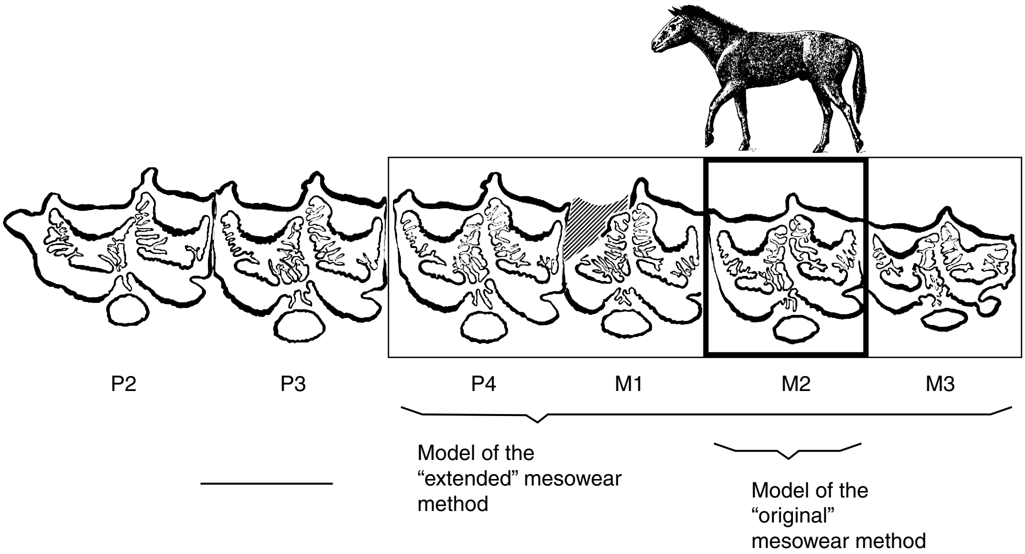

FIG. 7. — Occlusal aspect of the upper cheek tooth dentition of *Hippotherium primigenium* Meyer, 1829 from the Vallesian (MN9) Dinotheriensande (specimen HLMD-DIN 1076). Note the high degree of uniformity in the enamel ridge pattern of the individual cheek tooth positions. The model position of the "original" mesowear method after Fortelius & Solounias (2000) is the M2 (bold box). The model tooth positions for the proposed "extended" mesowear method are the tooth positions P4, M1, M2 and M3. Scale bar: 20 mm.

tion. This sensitivity is useful regarding the assemblage which consequently is a well suited one for the purpose of testing different models;

– 2) the observation that P2 and P3 cause a shift of the classification towards the more abrasion dominated side of the mesowear spectrum (towards the "grazers") in all samples investigated is consistent with the observed chi-square probabilities (Fig. 5), which indicate smaller p-values in models comprising those two tooth positions than in models not comprising P2 and P3. We therefore conclude that those two tooth positions incur the largest degree of mesowear classification inconsistency of all teeth in the equid cheek tooth row. We conclude therefore that P2 and P3 should be excluded from the extended mesowear methodology;

– 3) the observation that the two tested 3 and 4-tooth models (P4-M3 and P4+M2+M3) consistently classify in close neighborhood, in all recent and fossil samples investigated and mostly classify with the same recent reference species as the M2 is interpreted as strong evidence, that both models provide a dietary classification consistent with the classification of the original mesowear method. Differences in the recent reference species as observed in the We, Es and ebS samples are to be explained due to the comparably small numbers of M2 specimens available. This should turn the M2 signal little consistent.

Based on these observations, the 3 and 4-tooth models appear equally suited to act as the model for the "extended" mesowear method. The 5-tooth model tested however shows inconsistency which becomes evident in the southern sample of *Equus burchelli*, and therefore is not considered as a potential reference model.

The decision upon which of the both remaining models to propose therefore may be only based upon the number of tooth specimens.

Compared to the 3-tooth model (P4+M2+M3), the 4-tooth model (P4-M3) comprises one more tooth position. Instead of 121 specimens in the Dinotheriensande assemblage, 167 tooth specimens would be available in the 4-tooth model proposed (Fig. 5A). This qualifies the 4-tooth model (P4+M1+M2+M3) as the model for the "extended" mesowear method (Fig. 7). We have tested the proposed model using samples of fossil and recent hypsodont horses as references and we therefore expect the method to provide most reliable dietary classifications for this particular group of ungulates. Testing models for other ungulate groups, in particular the bovids, rhinocerotids and giraffids is currently the subject to further investigations.

THE PALEODIET OF *H. PRIMIGENIUM* FROM THE VALLESIAN DINOTHERIENSANDE

The present analysis shows that *H. primigenium* classifies with the following grazers: *Hippotragus niger* (hn), *Redunca redunca* (rr), *Hippotragus equinus* Desmarest, 1804 (he) and *Kobus ellipsiprymnus* (ke) (Fig. 8; a study based on 167 molars and premolars). This result is different from Kaiser *et al.* (2000a) where *H. primigenium* was classified as a mixed feeder similar to *Aepyceros melampus* (a study based on 20 upper molars). The difference in results can be attributed in methodology and in sample size.

Although, the paleodietary reconstruction of *H. primigenium* is not the focus of this study, we find that grass dominated the diet of *H. primigenium* at the Dinotheriensande localities. The population from the Dinotheriensande is therefore similar in dietary preferences to a close relative, *Cormohipparion occidentale* from Nebraska. Hayek *et al.* (1992) suggest the diet of *C. occidentale* to be that of a grazer on a single tooth (an older study when microwear was just beginning to be explored). Solounias, however, finds *C. occidentale* from Nebraska to be a mixed feeder (unpublished new microwear data of 17 individuals). We recognize that the results are on different species, continents, and time and more especially on different methods of investigation (mesowear versus microwear). Whether mixed feeder or grazer studies show the intake of substantial amounts of grass by species of *Cormohipparion* Skinner & MacFadden, 1977.

It was recognized, that the European (MN9) *Hippotherium primigenium* was morphologically very similar to *C. occidentale* (Bernor *et al.* 1997), which suggests similar diets as well. While *C. occidentale* was recognized from North America, *H. primigenium* appears in Europe close to the FAD (First Appearance Datum) of hipparionine horses at 11.2 m.a. (Bernor *et al.* 1996). An immigration of hypsodont hipparionine horses into Eurasia from North America initiated the most species diverse and ecologically meaningful radiation of Eurasian and African equids in the Miocene known. The fact that *H. primigenium* was a widely distributed European species and in some habitats likely incorporated a considerable amount of grass in its diet may reflect dietary regimes of some equids species in Europe during the MN9. Central Europe during the MN9 was characterized by mesophytic forests and more or less subtropical/warm temperate woodland conditions (Bernor *et al.* 1988), which were different

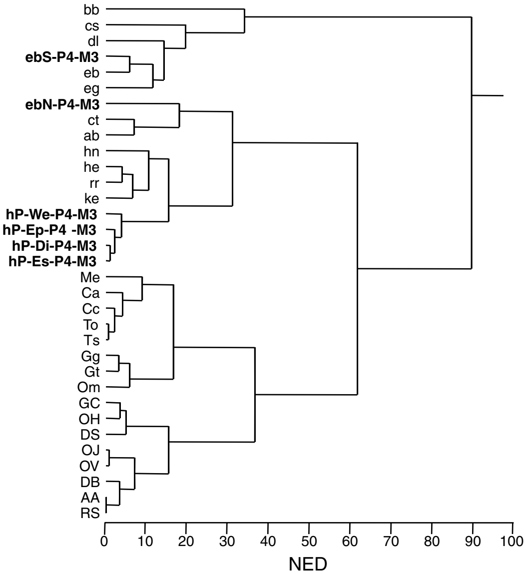

FIG. 8. — Hierarchical cluster diagram based on the mesowear variables %high (percent high occlusal relief), %sharp (percent sharp cusps) and %blunt (percent blunt cusps) based on the 4-tooth model (P4-M3) proposed as the model for the "extended" mesowear method in this study. Clusters based on a set of 27 "typical" recent comparison taxa after Fortelius & Solounias (2000). For abbreviations see Table 1; **upper case**, browser; **lower case**, grazer, **mixed case (capital first)**, mixed-feeder; **mixed case (lower first)**, fossil species; **NED**, normalised Euclidean distance.

from the more "savanna-like" conditions that were resident in North America at the same time. In forests grass can grow in riverine or hilly margins as well as in clearings. In conclusion, in North American and Central European Miocene habitats sufficient grass can occur which would allow for the observed scenarios of grazers or mixed feeders.

Acknowledgements

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APPENDIX

A) Specimen list of sample ebN representing 32 individuals of recent *Equus burchelli* Gray, 1824 curated at the American Museum of Natural History, New York (AMNH) and the Forschungsinstitut Senckenberg, Frankfurt am Main (SMF). All 182 cheek tooth specimens investigated belong to wild shot animals from Sudan, Kenya and Tanzania.

AMNH-118612, AMNH-119663, AMNH-119671, AMNH-119672, AMNH-164127, AMNH-165063, AMNH-187799, AMNH-187800, AMNH-187801, AMNH-204045, AMNH-216357, AMNH-216358, AMNH-27742, AMNH-27743, AMNH-27745, AMNH-27747, AMNH-27749, AMNH-27750, AMNH-27751, AMNH-39948, AMNH-542416, AMNH-54287, AMNH-82041, AMNH-82170, AMNH-82171, AMNH-82311, AMNH-83451, AMNH-85160, AMNH-85177.
SMF-16066, SMF-19209, SMF-19210.

B) Specimens list of sample ebS representing 23 individuals of wild shot recent *Equus burchelli* from Botswana, Namibia and Angola. 117 upper cheek tooth specimens curated at the AMNH are investigated.

AMNH-165055, AMNH-165057, AMNH-165058, AMNH-165059, AMNH-165060, AMNH-165061, AMNH-165062, AMNH-165064, AMNH-165065, AMNH-80593, AMNH-80594, AMNH-80596, AMNH-82312, AMNH-82313, AMNH-82314, AMNH-82315, AMNH-82316, AMNH-83452, AMNH-83453, AMNH-83455, AMNH-83456, AMNH-83457, AMNH-83601.

C) Specimen list of upper cheek teeth of *Hippotherium primigenium* Meyer, 1829 from the Vallesian (MN9) Dinotheriensande (Germany) investigated. HLMD-DIN-1076 is the only complete upper cheek tooth dentition from the Dinotheriensande known to the authors and comprises six dental specimens, the remaining specimens are isolated cheek teeth. Abbreviations: HLMD, Hessisches Landesmuseum, Darmstadt; LMM, Landesmuseum, Mainz; LSNK, Landessammlungen für Naturkunde, Karlsruhe; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main.

HLMD-DIN-1076, HLMD-DIN-1077, HLMD-DIN-1079, HLMD-DIN-2064, HLMD-DIN-2437, HLMD-DIN-2438, HLMD-DIN-2439, HLMD-DIN-2440, HLMD-DIN-2441, HLMD-DIN-2442, HLMD-DIN-2443, HLMD-DIN-2444, HLMD-DIN-2445, HLMD-DIN-2447, HLMD-DIN-2448, HLMD-DIN-2449, HLMD-DIN-2473, HLMD-DIN-2478, HLMD-DIN-2479, HLMD-DIN-2480, HLMD-DIN-2482, HLMD-DIN-2484, HLMD-DIN-2485, HLMD-DIN-2486, HLMD-DIN-2487, HLMD-DIN-2514, HLMD-DIN-2515, HLMD-DIN-2516, HLMD-DIN-2517, HLMD-DIN-2518, HLMD-DIN-2519, HLMD-DIN-2548, HLMD-DIN-2549, HLMD-DIN-2550, HLMD-DIN-2551, HLMD-DIN-2552, HLMD-DIN-2553, HLMD-DIN-2554, HLMD-DIN-2555, HLMD-DIN-2556, HLMD-DIN-2557, HLMD-DIN-2584, HLMD-DIN-2586, HLMD-DIN-2600, HLMD-DIN-2615, HLMD-DIN-2616, HLMD-DIN-2617, HLMD-DIN-2618, HLMD-DIN-2618, HLMD-DIN-2619, HLMD-DIN-2620, HLMD-DIN-2621, HLMD-DIN-2622, HLMD-DIN-2623, HLMD-DIN-2654, HLMD-DIN-2660, HLMD-DIN-2661, HLMD-DIN-2662, HLMD-DIN-2663, HLMD-DIN-2678, HLMD-DIN-2679, HLMD-DIN-2679, HLMD-DIN-2680, HLMD-DIN-2681, HLMD-DIN-2682, HLMD-DIN-2683, HLMD-DIN-2684, HLMD-DIN-2686, HLMD-DIN-2689, HLMD-DIN-2691, HLMD-DIN-2692, HLMD-DIN-2694, HLMD-DIN-2695, HLMD-DIN-2696, HLMD-DIN-2697, HLMD-DIN-2698, HLMD-DIN-2699, HLMD-DIN-2701, HLMD-DIN-2702, HLMD-DIN-2709, HLMD-DIN-2711, HLMD-DIN-2712, HLMD-DIN-2713, HLMD-DIN-2714, HLMD-DIN-2715, HLMD-DIN-2716, HLMD-DIN-2717, HLMD-DIN-2718, HLMD-DIN-2719, HLMD-DIN-2720, HLMD-DIN-2721, HLMD-DIN-2723, HLMD-DIN-2724, HLMD-DIN-2725, HLMD-DIN-2733, HLMD-DIN-2735, HLMD-DIN-2739, HLMD-DIN-2740, HLMD-DIN-2741, HLMD-DIN-2742, HLMD-DIN-2745, HLMD-DIN-2755, HLMD-DIN-2756, HLMD-DIN-2757, HLMD-DIN-2758, HLMD-DIN-2759, HLMD-DIN-2761, HLMD-DIN-2763, HLMD-DIN-2764, HLMD-DIN-2790, HLMD-DIN-2808, HLMD-DIN-2814, HLMD-DIN-2815, HLMD-DIN-2816,

HLMD-DIN-2817, HLMD-DIN-2820, HLMD-DIN-2824, HLMD-DIN-2825, HLMD-DIN-2826, HLMD-DIN-2827, HLMD-DIN-2828, HLMD-DIN-2829, HLMD-DIN-2830, HLMD-DIN-2831, HLMD-DIN-2832, HLMD-DIN-2833, HLMD-DIN-2834, HLMD-DIN-2836, HLMD-DIN-2837, HLMD-DIN-2838, HLMD-DIN-2840, HLMD-DIN-2845, HLMD-DIN-2857, HLMD-DIN-2858, HLMD-DIN-2859, HLMD-DIN-2860, HLMD-DIN-2861, HLMD-DIN-2869, HLMD-DIN-2878, HLMD-DIN-2880, HLMD-DIN-2881, HLMD-DIN-2882, HLMD-DIN-2902, HLMD-DIN-2903, HLMD-DIN-2904, HLMD-DIN-2905, HLMD-DIN-2906, HLMD-DIN-2907, HLMD-DIN-2911, HLMD-DIN-2912, HLMD-DIN-2913, HLMD-DIN-2914, HLMD-DIN-2917, HLMD-DIN-2918, HLMD-DIN-2919, HLMD-DIN-2920, HLMD-DIN-2921, HLMD-DIN-2923, HLMD-DIN-2924, HLMD-DIN-2925, HLMD-DIN-2926, HLMD-DIN-2929, HLMD-DIN-2930, HLMD-DIN-2930, HLMD-DIN-2932, HLMD-DIN-2933, HLMD-DIN-2934, HLMD-DIN-2940, HLMD-DIN-2941, HLMD-DIN-2943, HLMD-DIN-2947, HLMD-DIN-2951, HLMD-DIN-2952, HLMD-DIN-2953, HLMD-DIN-2957, HLMD-DIN-2960, HLMD-DIN-2961, HLMD-DIN-2962, HLMD-DIN-2970, HLMD-DIN-2971, HLMD-DIN-2974, HLMD-DIN-2975, HLMD-DIN-2976, HLMD-DIN-2977, HLMD-DIN-2979, HLMD-DIN-2980, HLMD-DIN-2983, HLMD-DIN-2987, HLMD-DIN-2991, HLMD-DIN-3005, HLMD-DIN-3013, HLMD-DIN-3022, HLMD-DIN-3023, HLMD-DIN-3024, HLMD-DIN-3175, HLMD-DIN-3176, HLMD-DIN-3177, HLMD-DIN-3569, HLMD-DIN-3570, HLMD-DIN-3571, HLMD-DIN-3572, HLMD-DIN-3573, HLMD-DIN-3574, HLMD-DIN-3575, HLMD-DIN-3576, HLMD-DIN-3577, HLMD-DIN-3578, HLMD-DIN-3579, HLMD-DIN-3581, HLMD-DIN-3582, HLMD-DIN-3583, HLMD-DIN-3584, HLMD-DIN-3585, HLMD-DIN-3587, HLMD-DIN-3588, HLMD-DIN-3589, HLMD-DIN-3590, HLMD-DIN-3591, HLMD-DIN-3592, HLMD-DIN-3597, HLMD-DIN-3599, HLMD-DIN-3600, HLMD-DIN-3601, HLMD-DIN-3602, HLMD-DIN-3603, HLMD-DIN-3604, HLMD-DIN-3605, HLMD-DIN-3606, HLMD-DIN-3607, HLMD-DIN-3608, HLMD-DIN-3610, HLMD-DIN-3611, HLMD-DIN-3612-, HLMD-DIN-3613, HLMD-DIN-3614, HLMD-DIN-3616, HLMD-DIN-3617, HLMD-DIN-3618, HLMD-DIN-3619, HLMD-DIN-3620, HLMD-DIN-3621, HLMD-DIN-3622, HLMD-DIN-3623, HLMD-DIN-3624, HLMD-DIN-3626, HLMD-DIN-3627, HLMD-DIN-3628, HLMD-DIN-3629, HLMD-DIN-3630, HLMD-DIN-3631, HLMD-DIN-3632, HLMD-DIN-3633, HLMD-DIN-3634, HLMD-DIN-3635.

LSNK-10A, LSNK-11A, LSNK-13A, LSNK-14A, LSNK-15A, LSNK-16A, LSNK-17A, LSNK-18A, LSNK-19A, LSNK-1A, LSNK-1Bb, LSNK-20A, LSNK-21A, LSNK-22A, LSNK-23A, LSNK-24A, LSNK-25A, LSNK-26A, LSNK-27A, LSNK-28A, LSNK-29A, LSNK-2A, LSNK-2Bb, LSNK-30A, LSNK-31A, LSNK-33A, LSNK-34A, LSNK-35A, LSNK-36A, LSNK-3A, LSNK-4A, LSNK-5A, LSNK-6A, LSNK-7A, LSNK-8A, LSNK-9A.

LMM-PW-1998/10000LS, LMM-PW-1998/10001LS, LMM-PW-1999/10048-LS.

SMF-M1023A, SMF-M1043, SMF-M1043B, SMF-M1050, SMF-M1082, SMF-M1091A, SMF-M1091B, SMF-M1091C, SMF-M1430, SMF-M1431, SMF-M1432, SMF-M2730, SMF-M4800B, SMF-TMK1, SMF-TMK10, SMF-TMK11, SMF-TMK12, SMF-TMK14, SMF-TMK16, SMF-TMK18, SMF-TMK19, SMF-TMK2, SMF-TMK20, SMF-TMK21, SMF-TMK22, SMF-TMK24, SMF-TMK26, SMF-TMK27, SMF-TMK28, SMF-TMK29, SMF-TMK3, SMF-TMK30, SMF-TMK31, SMF-TMK32, SMF-TMK33, SMF-TMK34, SMF-TMK35, SMF-TMK37, SMF-TMK4, SMF-TMK5, SMF-TMK6, SMF-TMK7, SMF-TMK8, SMF-TMK9.