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# The dietary regimes of two contemporaneous populations of *Hippotherium primigenium* (Perissodactyla, Equidae) from the Vallesian (Upper Miocene) of Southern Germany

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## Abstract

The first occurrence of tridactyl, hipparionine horses is presently constrained in Eurasia between 11.2 and 10.8 Myr. *Hippotherium primigenium* is the only species recorded up to now in the early Vallesian–early Turolian of Germany. Two Vallesian populations of *H. primigenium* are investigated with respect to their trophic regimes. One of these populations derives from the deposits of the Upper Miocene Rhine river exposed at the locality of Eppelsheim (Germany). The other population (Höwenegg) is represented by lacustrine deposits of a former crater lake about 180 km south of Eppelsheim. Both localities represent two almost contemporaneous Vallesian (MN9) populations of a single equid taxon (*H. primigenium*) from different geographic regions within western Germany. Trophic regimes are reconstructed using the mesowear method [Fortelius and Solounias, *Am. Mus. Novit.* 3301 (2000) 1–36] and the derived ‘extended’ mesowear method [Kaiser and Solounias, *Geodiversitas* (2003), in press]. These analyses lead to the identification of a recent trophic reference taxon for each of the two hipparion populations. The common waterbuck (*Kobus ellipsiprymnus*), a grazer inhabiting reed beds and also foraging into woodlands is identified as the trophic analog for the Eppelsheim population. The reference taxon of the Höwenegg population is the Sumatran rhinoceros (*Dicerorhinus sumatrensis*), a browser, inhabiting mainly hilly country and preferring saplings, fruit, leaves, twigs, and bark as major food items. The marked differences in the trophic regimes found for the two populations of *H. primigenium* are interpreted as reflecting the range of possible dietary regimes, here termed the trophic spectrum of this equid species. The trophic signal of *H. primigenium* is therefore interpreted as an ecological signal reflecting properties of the habitat. The paleohabitat of Eppelsheim would then be recognized as representing at least seasonally extended grassy areas such as reed flats in the proximity of the Miocene Rhine river. The paleohabitat of the Höwenegg, however, was most likely an immediate part of the subtropical mesophytic forests, that covered large parts of Central and Western Europe, Central Asia and southern China during the Vallesian period.

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**Keywords:** hipparion; Miocene; paleodiet; mesowear; paleoecology

**Abbreviations:** HLMD, Hessisches Landesmuseum, Darmstadt; NED, normalized Euclidean distance (root-mean-squared)

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## 1. Introduction

Neogene Old World equids are all derived from North American ancestors that dispersed into

Eurasia across Beringia during times of eustatic sea-level lowering. The first occurrence of tridactyl, hipparionine horses with moderately hypsodont cheek teeth is presently well constrained in Eurasia between 11.2 and 10.8 Myr. *Hippotherium primigenium* is at present the only species recorded in the early Vallesian–early Turolian of Germany and is the prevalent Vallesian hipparion in the Central Paratethys (Bernor et al., 1988, 1993a,b, 1997; Bernor and Franzen, 1997). The genotype species *H. primigenium* originates from the locality of Eppelsheim, western Germany, within the Dinotheriensande complex (Bernor et al., 1996), but is best known by complete skeletons from the Höwenegg (Hegau), southern Germany (Bernor et al., 1997). *H. primigenium* is remarkable for its large size (equalling a Burchell's zebra in stature), gracile build and its axial skeleton adapted for leaping and springing rather than high speed, and sustained running (Bernor and Armour-Chelu, 1999). It was a horse well adapted to Central Europe's Vallesian subtropical-to-warm temperate woodland environments (Bernor et al., 1997; Kaiser et al., 2000a). In this study the dietary preferences of two populations of *H. primigenium* from the two localities of Eppelsheim (EP) and Höwenegg (HO) in Germany are investigated. Both localities represent two almost contemporaneous Vallesian (MN9) populations of a single equid taxon from different geographic regions within western Germany. This study presents rarely gained information about the trophic spectrum (range of possible dietary regimes) of a fossil taxon and on differential habitat conditions in the Vallesian period of this geographic region.

Investigations on the paleodiet of Neogene hipparionines from Eurasia were undertaken by using a variety of methods, including stable isotopes, microwear and mesowear (e.g. Bernor et al., 1999; Bernor and Armour-Chelu, 1999; Caprini, 1998; Cerling et al., 1997; Eisenmann, 1998; Fortelius and Solounias, 2000; Hayek et al., 1992; Kaiser et al., 2000a,b; Kaiser and Bernor, 2001; Kaiser and Solounias, 2003; Kaiser et al., 2001; Kaiser et al., 2003 (in press); MacFadden and Cerling, 1996; Solounias and Semprebon, 2002). These investigations revealed an impressive dietary diversity in European and Asian Neogene

hipparionines, which covers the entire spectrum between extreme grazing and exclusive browsing.

## 2. The mesowear method

A new approach to reconstructing ungulate diet, the mesowear method was introduced by Fortelius and Solounias (2000). Mesowear is based on facet development on the occlusal surfaces of the cheek 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 can be used to reconstruct ungulate diets (Fortelius and Solounias, 2000). The mesowear method treats ungulate tooth mesowear as two variables: occlusal relief and cusp shape. Occlusal relief (OR) 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. Kaiser et al. (2000a) tested the mesowear method in a blind test study, and calibrated it for potential observer error in scoring mesowear traits. The method was found to be consistent and robust. The mesowear method after Fortelius and Solounias (2000) investigates mesowear using the upper second molar ( $M^2$ ) as a model (one-tooth model). Fortelius and Solounias found the method to provide stable trophic classifications, if a minimum of 20 tooth individuals is investigated. For use in hypsodont equids, Kaiser and Solounias (2003) extend the method to four tooth positions ( $P^4$ – $M^3$ ) (four-tooth model). This makes the method available for fossil assemblages, which mostly consist of relatively small numbers of tooth individuals assignable to a certain tooth position. This extension now makes a wide range

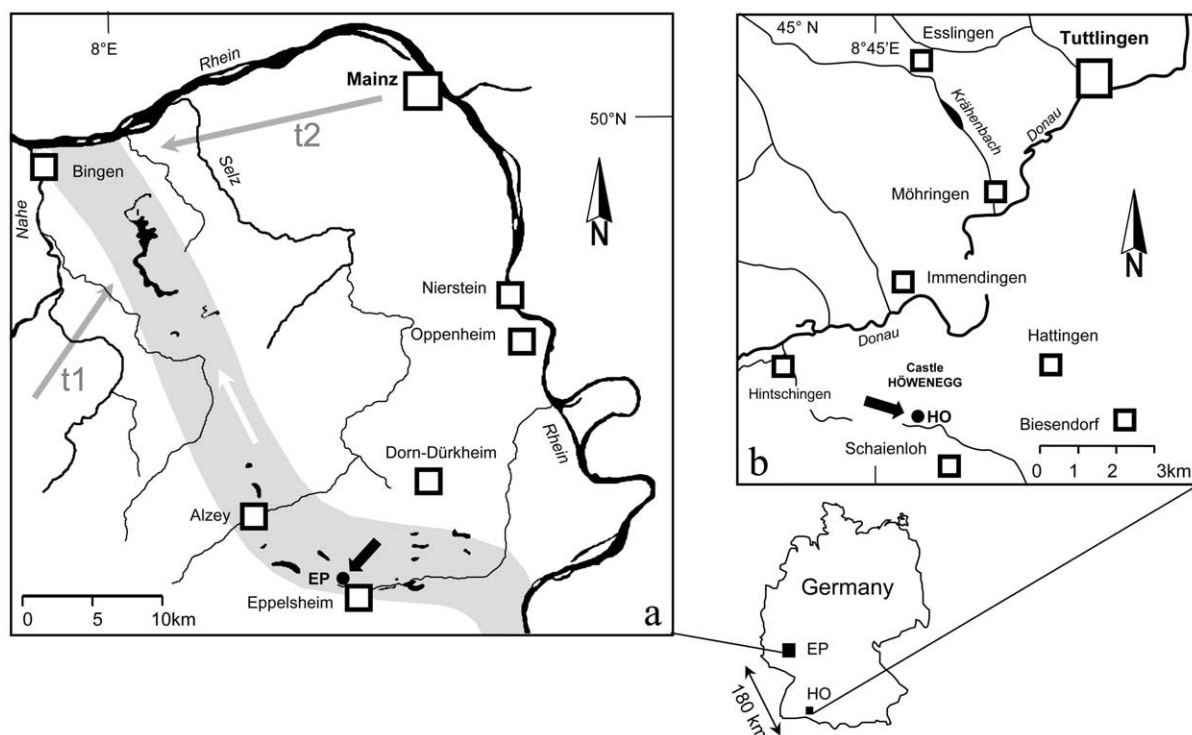


Fig. 1. (a) Geographic situation of the Vallesian (MN9) fossil localities of the Dinotheriensande (black signatures). Black arrow, locality of Eppelsheim (EP); gray lines indicate the approximate course of Upper Miocene rivers; t1 and t2, proposed tributaries of the main river, the Miocene Rhine river (after Franzen, 1997 and Tobien, 1983). (b) The Höwenegg locality in Southern Germany. The Höwenegg beds represent a lake deposit that is presently exposed at the hillside of the former Höwenegg volcano situated south of the village of Immendingen (after Bernor et al., 1997). Black arrow, locality of Höwenegg (HO).

of fossil equid populations accessible to mesowear investigation, and allows one to reconstruct and compare the dietary regime of different populations of a certain fossil species.

### 3. Materials and methods

In this study we apply the ‘extended mesowear method’ after Kaiser and Solounias (2003), which evaluates mesowear using four positions of upper maxillary cheek teeth. In order to attain consistency with the approach of Fortelius and Solounias (2000) and Kaiser and Solounias (2003), tooth specimens not yet in occlusion and specimens showing initial wear are excluded, as well as specimens with a persisting crown height of less than 15 mm. The tooth crowns of all specimens were molded with Provil Soft dental mold-

ing putty (Bayer). Casts were made using Injektionsharz EP epoxy resin (Reckli). All scoring was done using plastic casts rather than the original specimens. Teeth were scored after the convention by Fortelius and Solounias (2000) and absolute and relative frequencies (percentages) of mesowear variables were calculated for each population investigated. Scoring was based on the tooth positions  $P^4$ – $M^3$ , the reference positions of the ‘extended’ mesowear method after Kaiser and Solounias (2003) (four-tooth model) and the  $M^2$ , the reference position of the ‘original’ mesowear method after Fortelius and Solounias (2000) (one-tooth model) independently (Tables 1, 2 and 4).

#### 3.1. The reference species

Fortelius and Solounias (2000) use 64 recent

Table 1

Tooth specimens from the Eppelsheim population of *Hippotherium primigenium* investigated, sorted by tooth position and increasing crown height

SPEC_ID	BONE	SIDE	M5	OR	CS	WEAR
SMF-TMK35	txP4	l	20.36	h	r	3
HLMD-DIN-2808	txP4	l	22.2	l	r	3
HLMD-DIN-2720	txP4	l	23.3	h	r	3
HLMD-DIN-2615	txP4	r	25.9	h	r	3
SMF-M1043	txP4	r	32.4	h	r	3
HLMD-DIN-2725	txP4	r	33	h	r	3
SMF-M1432	txP4	l	33.5	h	–	3
SMF-M1431	txP4	l	36.2	h	s	3
SMF-TMK10	txP4	r	36.89	h	r	3
SMF-TMK30	txP4	r	37.82	h	r	3
SMF-M1091A	txP4	l	40.2	h	r	3
HLMD-DIN-2828	txP4	l	41.3	h	s	3
HLMD-DIN-2918	txP4	l	42.6	h	r	3
HLMD-DIN-2837	txP4	r	44.3	h	s	3
HLMD-DIN-2814	txP4	l	44.7	h	r	3
HLMD-DIN-2721	txP4	r	45.1	h	s	3
HLMD-DIN-2739	txP4	r	46	h	r	3
SMF-M2730	txP4	l	46.1	h	r	3
SMF-TMK27	txP4	l	48.76	h	–	3
HLMD-DIN-2745	txP4	r	50.9	h	r	2
HLMD-DIN-2838	txP4M1	r	34.1	h	–	3
SMF-TMK18	txM1	l	16.57	h	r	3
HLMD-DIN-2622	txM1	l	17.4	h	r	3
HLMD-DIN-2718	txM1	r	18.6	h	r	3
HLMD-DIN-2919	txM1	l	18.7	h	r	3
SMNK1Bb	txM1	l	21.7	h	r	3
SMF-M1091B	txM1	l	24.6	h	r	3
HLMD-DIN-1077	txM1	l	26.9	h	r	3
SMF-TMK31	txM1	l	28.52	h	r	3
HLMD-DIN-2833	txM1	r	34.2	h	s	3
SMF-TMK19	txM1	r	35.52	l	–	3
HLMD-DIN-2621	txM1	r	36.9	h	r	3
SMF-TMK7	txM1	r	38.55	h	r	3
HLMD-DIN-2715	txM1	l	39.4	h	s	3
HLMD-DIN-2830	txM1	l	42.2	h	–	3
HLMD-DIN-2719	txM1	r	42.5	h	r	3
HLMD-DIN-2735	txM1	r	42.6	h	r	3
LMM-PW-1998/10000LS	txM1	r	43.45	h	s	3
HLMD-DIN-2616	txM1	r	47	h	r	2
SMF-TMK11	txM1	r	47.39	h	–	2
HLMD-DIN-2759	txM1	r	50	h	r	3
SMF-TMK28	txM1	l	51.24	h	r	2
LMM-PW-1999/10048LS	txM2	l	24.9	h	r	3
HLMD-DIN-2761	txM2	r	26.8	h	r	3
HLMD-DIN-2716	txM2	r	32	h	r	3
HLMD-DIN-2763	txM2	l	39.4	h	r	3
SMF-M1430	txM2	l	44.3	h	r	3
HLMD-DIN-2757	txM2	r	45.3	h	r	3
HLMD-DIN-2815	txM2	l	50.2	h	r	2
SMF-M1091C	txM3	l	18.6	h	–	3
SMF-M1043B	txM3	r	21.8	h	s	3
HLMD-DIN-2618	txM3	r	25.5	h	r	3

Table 1 (Continued).

SPEC_ID	BONE	SIDE	M5	OR	CS	WEAR
SMF-TMK6	txM3	l	26.58	h	r	3
SMF-TMK1	txM3	l	32.23	h	r	3
SMF-TMK20	txM3	l	35.31	h	r	3
HLMD-DIN-2623	txM3	r	37.9	h	r	3
HLMD-DIN-2764	txM3	r	40	h	r	2
HLMD-DIN-2816	txM3	r	41.2	h	r	3

SPEC\_ID = specimen identification, BONE = tooth position (tx = tooth maxillary), SIDE = side (r = right, l = left), M5 = crown height [mm] (convention of Eisenmann et al., 1988 and Bernor et al., 1997), OR = occlusal relief (l = low, h = high), CS = cusp shape (s = sharp, r = round), WEAR = wear stage (definition after Kaiser et al., 2003, in press). SMF = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany; SMNK = Staatliches Museum für Naturkunde, Karlsruhe, Germany; LMM = Landesmuseum Mainz, Mainz, Germany.

ungulate species with known diets as a reference in their analyses. Among these were species with variously problematic diets (namely the water chevrotain, the duikers and the hyraxes), which made up together the ‘mabra’ group of ‘minute abraded brachydont’. These species were excluded in the present study. Analysis was thus undertaken using a set of 54 recent comparison taxa exclusively of the ‘mabra’ group, and additionally a reduced set of 27 ‘typical’ recent species as a comparative set, which have been shown to provide reliable dietary data without anomalies. Fortelius and 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) and the resolution of the method increased as it was included. The index of hypsodonty (from Janis, 1988) was not included in this study because it requires crown height measurements, which are not available in the Höwenegg assemblage due to the complete preservation of articulated skulls at this locality. Of the several dietary classifications Fortelius and Solounias tested, the conservative classification resulted in the most correct classification of species based on mesowear variables and the index of hypsodonty. The contribution follows their classification of extant species into the three broad dietary categories browser, mixed feeder, and grazer. In the Eppelsheim specimens molar crown height was measured according to the conventions of Eisenmann et al. (1988) and Bernor et al. (1997). All measurements were taken twice using dial calipers, averaged and rounded to 0.1 mm.

### 3.2. Statistics

The  $\chi$ -square tests were performed to test for significance in differences observed in the distribution patterns of mesowear variables of the two assemblages of *H. primigenium*. Hierarchical cluster analysis with complete linkage (furthest neighbor) was applied following the standard hierarchical amalgamation method of Hartigan (1975). The algorithm of Gruvaeus and Wainer (1972) was used to order the tree. The three mesowear variables perhigh, persharp and perblunt were used. For this analysis we used the original dataset of Fortelius and Solounias (2000) for the extant comparison species and the data presented in this study for the fossil populations of *H. primigenium*. Statistical tests were computed using Systat 9.0 and Axum 6 software.

### 3.3. The populations of Vallesian Hippotherium primigenium investigated

#### 3.3.1. The Eppelsheim sample of *H. primigenium*

Deposits of the Miocene Rhine river are exposed at many places in the Rheinhessen area, West Germany (Fig. 1). This Upper Miocene sequence of sands, silts, gravels and conglomerates, which have been extensively quarried during the 19th and early 20th centuries, have yielded a rich mammalian fauna, which is known as the Dinotheriensandfauna (Tobien, 1980, 1983). The Dinotheriensande localities are all placed within the lower part of MN9, the age of which is estimated at about 10.5 Myr (Steininger et al., 1996; An-

draws and Bernor, 1999). From the numerous localities of the Dinotheriensande, the locality of Eppelsheim is situated 30 km south of the city of Mainz. It is the only site that is still scientifically excavated by the Forschungsinstitut Senckenberg, Frankfurt and the Naturkundemuseum of the city of Mainz (Franzen, 2000; Franzen et al., in press). Eppelsheim has yielded the richest assemblage of mammalian remains from a specific Dinotheriensande locality and therefore is the best investigated single assemblage from the Dinotheriensande complex. Additionally, this assemblage comprises the genotypic sample of *H. primigenium* (Meyer, 1829), which is presently housed at the Forschungsinstitut Senckenberg (Frankfurt) (Franzen, 2000; Kaiser et al., 2003, in press). The chronological homogeneity of the Dinotheriensande sample is uncertain, but there is no reason to believe at present that more than one species of hipparions is present in this sample. Besides being the largest sample of teeth known of *H. primigenium*, the Dinotheriensande sample, with the exception of one associated upper cheek dentition (Hessisches Landesmuseum, Darmstadt, Germany (HLMD)-DIN-1076) and one mandible (HLMD-DIN-1081), is known entirely from isolated teeth allowing crown height measurements to be taken, which is important for ultimately knowing the wear stage and age of the individual at death. The latter facts make Eppelsheim the most favorable reference sample for the Dinotheriensande complex.

The sample investigated comprises a total of 119 maxillary cheek tooth specimens assignable to *H. primigenium*. After excluding specimens in very early wear, and specimens with less than 15 mm crown height remaining, in the Eppelsheim sample 104 tooth specimens of all six cheek tooth positions were available for this investigation. The tooth positions crucial for the four-tooth model of the 'extended mesowear method' ( $P^4-M^3$ ) comprise 58 tooth individuals; the  $M^2$  (the reference position of the 'original' mesowear method (one-tooth model)), however, is represented by only seven specimens in this assemblage (Table 1).

The Dinotheriensande complex is a fluvial deposit. Mammalian fossils are almost entirely re-

Table 2

Tooth specimens of the Höweneegg population of *Hippotherium primigenium* investigated

SPEC_ID	BONE	SIDE	OR	CS	WEAR
HLMD-Ho58/V2	txP4	r	h	s	3
HLMD-Ho58/V2	txP4	l	h	r	3
Ho187G	txP4	r	h	s	3
Ho212	txP4	r	h	–	3
Ho53	txP4	r	h	s	3
Ho75554	txP4		h	s	3
HoA	txP4	l	h	–	3
HoA	txP4	r	h	s	3
HoB54	txP4	l	h	r	2
HoB54	txP4	r	h	–	2
HoI53	txP4	l	h	s	3
HoM55/1	txP4	r	h	s	3
RLB8574	txP4	r	h	s	3
HLMD-Ho58/V2	txM1	r	h	s	3
HLMD-Ho58/V2	txM1	l	h	s	3
Ho187H	txM1	l	h	r	3
Ho53	txM1	r	h	s	3
HoA	txM1	l	h	–	3
HoA	txM1	r	h	s	3
HoB54	txM1	l	h	–	3
HoB54	txM1	r	h	s	3
HoB54	txM1	r	h	s	3
HoI53	txM1	l	h	s	3
HoM55/1	txM1	r	h	s	3
HLMD-Ho58/V2	txM2	r	h	s	3
HLMD-Ho58/V2	txM2	l	h	s	3
Ho212	txM2	l	h	s	3
Ho53	txM2	r	h	r	3
HoA	txM2	l	h	r	3
HoA	txM2	r	h	s	3
HoB54	txM2	l	h	s	3
HoB54	txM2	r	h	r	3
HoI53	txM2	l	h	s	3
HoM55/1	txM2	r	h	s	3
HLMD-Ho58/V2	txM3	r	h	s	3
HLMD-Ho58/V2	txM3	l	h	r	3
Ho53	txM3	r	h	s	3
HoA	txM3	l	h	s	3
HoA	txM3	r	h	s	3
HoB54	txM3	l	h	s	2
HoB54	txM3	r	h	s	2
HoI53	txM3	l	h	r	3
HoM55/1	txM3	r	h	s	3
HoY59/5	txM3	r	h	s	3

SPEC\_ID = specimen identification, BONE = tooth position (tx = maxillary tooth), SIDE = side (r = right, l = left), OR = occlusal relief (h = high), CS = cusp shape (s = sharp, r = round), WEAR = wear stage (definition after Kaiser et al., 2003, in press).

stricted to a sand- and gravel-dominated horizon close to the base of the sequence (Tobien, 1983). Bartz (1936) reconstructed a SE–NW direction for the former course of the Dinotheriensande river system responsible for the deposition of the fossiliferous sediments (Fig. 1). Only very few remains of small mammals have been found in the Dinotheriensande so far (Franzen et al., in press). Based on the observation that large taxa predominate, Tobien (1983) argues for a rather high-energy depositional environment and for the absence of suitable ecological conditions, making owl pellets available for deposition. With rare exceptions associated skeletal elements are unknown. Tobien notes that the Dinotheriensande provide the rare opportunity to study a linear stream valley structure, with fossil localities spread along 26 km of its course. Tobien (1983) estimates the width of the meandering river system to be 8 km in the south, while it becomes more narrow in the north (4 km). The Eppelsheim locality is situated at the most proximal end of this structure, while towards the distal end two tributaries (t1 and t2, Fig. 1a) meet the main river. Towards the NW of this confluence, no further fossil occurrences seem to exist (Bartz, 1936). A leaf flora from the Dinotheriensande was recorded at the locality of Sprendlingen (Meller (1989), which consists of roughly 1000 leaf specimens. Among other taxa the flora includes *Ulmus*, *Salix*, *Betulaceae*, *Zelkova*, *Quercus*, *Taxodium*, *Acer*, *Populus* and *Fagus*. It represents a fraction of the most abundant members of a mixed mesophytic forest flora (Mai, 1981). Meller (1989) concludes that this flora represents a typical Neogene aue forest of the *Ulmus*–*Salix* type. No pollen floras have been recorded so far (Meller, 1989; Franzen, personal communication).

### 3.3.2. The Höwenegg sample of *Hippotherium primigenium*

The Upper Miocene fossil locality of Höwenegg (Hegau, southern Germany; Fig. 1b) has yielded articulated mammal skeletons as well as isolated skeletal elements from various species of Perissodactyla and Artiodactyla, among which the hipparionine equid *H. primigenium* is the most frequently preserved. The mammal remains are in

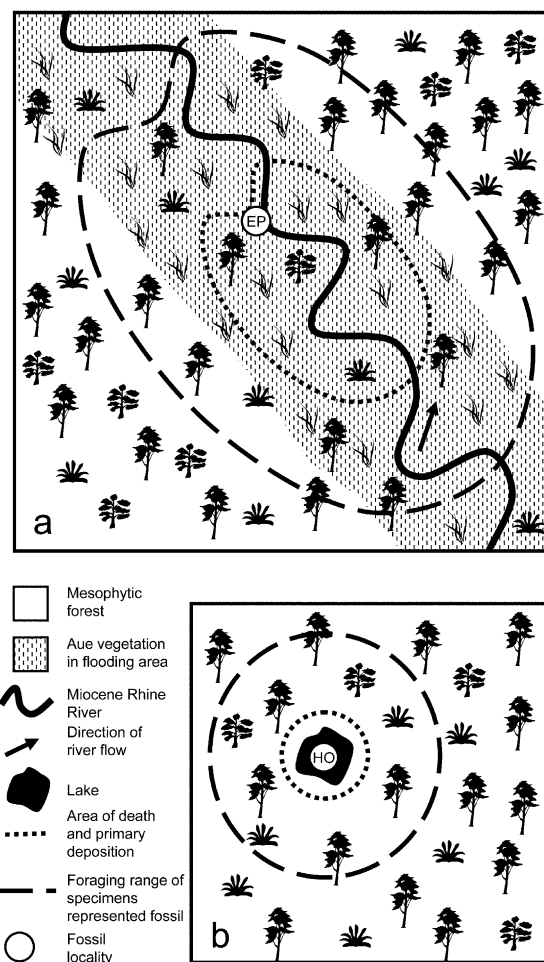


Fig. 2. Structure of the paleohabitats represented by the Dinotheriensande at Eppelsheim (a) and the Höwenegg-Schichten (b).

association with an invertebrate fauna as well as plant fossils.

It was suggested that the ‘Höwenegg-Schichten’ formed within a crater structure, which was built after the eruption of hornblende pyroclastics (Schreiner, 1976). These vulcanites pierced an older basalt complex, which is exposed about 800 m to the southeast of the locality. Subsequently, a sequence of lacustrine sediments consisting largely of carbonatitic tuffits filled the resulting depression. Recent chronostratigraphic work suggests an MN correlation which place the ‘Höwenegg-

Schichten' in the early Vallesian = MN9 (Berggren and van Couvering, 1974; Bernor et al., 1989; Bernor et al., 1988; Bernor et al., 1980; Mein, 1989; Steininger et al., 1989; Tobien, 1986). Radiometric dating by Lippolt et al. (1963) suggests an age of 7–6 Myr for the adjoining basalts and  $12.4 \pm 1$  Myr for a hornblende tuff from the Höwenegg profile. Weiskirchner (1975) dated an olivine nephelinite to  $11.8 \pm 0.6$  Myr, and the hornblende tuff to  $9.4 \pm 0.5$  Myr. Swisher (1996) provided a date of 10.3 Myr based on the hornblende tuff from the Höwenegg sequence.

Recent work by Woodburne et al. (1996b) has provided new geological data concerning the genesis of the Höwenegg sequence, which is proposed to represent a lacustrine deposit with periodical mudflows. The sequence originally had a thickness of about 12+ m, from which only the lowermost 4 m is preserved. Sedimentological investigations by Theobald (in Woodburne et al., 1996b) confirm Tobien's (1986) conclusion that the fossils accumulated in a shallow anaerobic lake. With the exception of periodical mudflows there was only little current. According to Bernor et al. (1997) there is evidence that the lake sediments have been deposited within a quite short geochronological interval.

Tobien (1986) interprets the articulated mammal skeletons as the remains of individuals that either drowned in the lake, or were transported there from a rather short distance as a whole. Tobien, however, points out that for numerous isolated skeletal elements found, a transport from a longer distance to the lake is supposed to have occurred (Tobien, 1986, p. 30). The plant remains are relatively abundant; however, they represent only a little diverse taphocoenosis (Gregor, 1982; Kirchheimer, 1957). Gregor emphasizes that the taxa identified show high correspondence with other Central European middle and Upper Miocene taxa. Tobien (1986) and Bernor et al. (1988) have shown that this flora, which is dominated by the Mediterranean genus *Celtis*, was a deciduous flora, showing a warm-temperate character, which is indicative of warm mesophytic forests with nominal seasonality. Tobien's (1986) paleoecological interpretations based on the mammalian fauna correspond with Gregor's (1982)

and Bernor et al.'s (1988) reconstruction of the Höwenegg paleohabitat.

Sixty-seven tooth specimens of all six cheek tooth positions were available from the Höwenegg *H. primigenium* assemblage. The tooth positions crucial for the four-tooth model of the 'extended mesowear method' ( $P^4-M^3$ ) comprise 43 tooth individuals (Table 2); the  $M^2$  (one-tooth model), however, is represented by only 10 specimens in this assemblage.

### 3.3.3. Concluding remarks on the paleoecology of the two Vallesian assemblages

The two localities Eppelsheim and Höwenegg are separated by a distance of 180 km, and populations of *Hippotherium primigenium* represent a narrow time frame within the MN9. The Höwenegg population is possibly up to 100,000–200,000 years younger than the Eppelsheim population. Both populations represent a single species of equid, *H. primigenium*. Regarding the homogeneity of the populations preserved, it is likely that in the Eppelsheim sample, there is more time averaging than in the Höwenegg assemblage. The area of origin of the individuals represented in the taphocoenosis is proposed to be larger for the Eppelsheim sample (Fig. 2a,b). The Eppelsheim specimens are almost entirely represented by isolated skeletal elements, while in the Höwenegg assemblage the teeth are still in the alveolae of the maxillary bones. Significant differences are evident in the taphonomic history of the two depositional environments and subsequently on the structure of the paleohabitats. The Eppelsheim habitat is most likely a riverine environment bordered by mesophytic deciduous aue forests of the *Ulmus-Salix* type (Fig. 2a). The Höwenegg habitat is considered a mesophytic forest habitat with no indication of the immediate proximity of a stream (Fig. 2b).

### 3.4. The possible influence of fluvial transport on the mesowear signal

In order to test if the dental specimens of *Hippotherium primigenium* from Eppelsheim have undergone a certain amount of sediment abrasion, a scanning electron microscope (SEM) investiga-



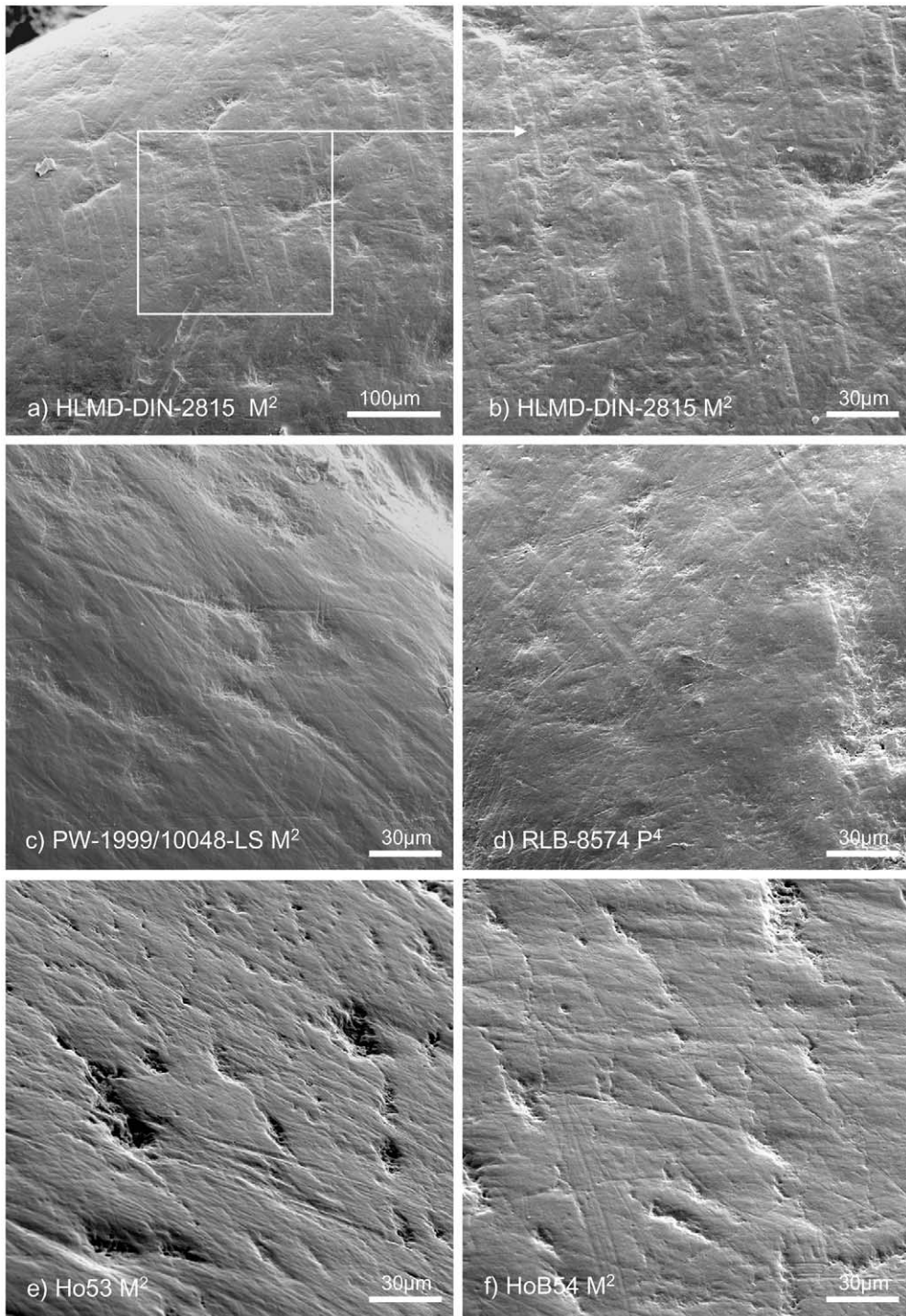


Fig. 3. SEM micrographs of cusp apices of upper cheek teeth of the population of *Hippotherium primigenium* from Eppelsheim (panels a–c) and Höwenegg (panels d–f).

Table 3  
The recent and fossil species in this study

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

Table 3 (Continued).

Sym	Species	Common name	Order	Family
To	<i>Taurotragus oryx</i>	eland	Artiodactyla	Bovidae
Tq	<i>Tetracerus quadricornis</i>	chousingha	Artiodactyla	Bovidae
Tr	<i>Boselaphus tragocamelus</i>	nilgai	Artiodactyla	Bovidae
Ts	<i>Tragelaphus scriptus</i>	bushbuck	Artiodactyla	Bovidae
hP	Extinct species <i>Hippotherium primigenium</i>		Perissodactyla	Equidae

Sym = abbreviations used to label species in cluster plots. Dietary classification follows the consensus classification of Fortelius and Solounias (2000).

tion of cusp apices was undertaken. There was no attempt made to quantify the possible indications of abrasion; instead a simple qualitative approach was favored. The buccal enamel band of the post-fossette, resulting when the metacone is worn, was investigated in 10 upper cheek tooth specimens of each sample. The overall appearance of the occlusal aspect of the cusp apices is inspected for characteristic microwear features (e.g. Hayek et al., 1992; Solounias and Hayek, 1993; Teaford and Robinson, 1989; Solounias et al., 1988) indicative of an occlusal surface with no post-mortem alterations. In this the procedure by Hayek et al. (1992), who investigated the flanks of the cusp apices in their microwear studies, is abandoned.

SEM investigation was carried out using the replica technique as described. After cleaning

specimens with acetone and varnish remover (Zip-Strip, Star Bronce Company, Alliance, Box 2206, OH 44601-0206, USA) (cf. Hayek et al., 1992), molds were taken using Provil novo Light C.D. (Heraeus Kulzer) polysiloxane dental molding material. Replicas were reversed using epoxy resin Injektionsharz EP (Recki-Chemiewerkstoff Co., 44629 Herne, Germany). The replicas were mounted on Al stabs, using conductive-C cement (Neubauer Chemikalien, 48031 Münster, Germany) and sputter-coated with 25 µm gold employing an Edwards Sputter Coater S15 0B. Investigation was carried out with a Zeiss DSM 940A scanning electron microscope at 4–5 kV. Images were processed digitally. Photographs were taken perpendicularly to the occlusal surface with a standard magnification of 500×.

Table 4

Mesowear variable distribution in the two populations of *Hippotherium primigenium* investigated

Locality	Sym	l	h	s	r	b	%l	%h	%s	%r	%b	Model
EP	hP (EP)	2	56	8	43	0	3	97	16	84	0	four-tooth model (P <sup>4</sup> -M <sup>3</sup> )
HO	hP (HO)	0	43	30	8	0	0	100	79	21	0	one-tooth model (M <sup>2</sup> )
EP	hP (EP)	0	7	0	7	0	0	100	0	100	0	
HO	hP (HO)	0	10	7	3	0	0	100	70	30	0	
Four-tooth model (P <sup>4</sup> -M <sup>3</sup> )		h,s,r: $\chi$ -square = 35.5477, df = 2, $P < 0.0001$ s,r: $\chi$ -square = 33.0788, df = 1, $P < 0.0001$ l,h: $\chi$ -square = 0.2578, df = 1, $P = 0.6117$										
One-tooth model (M <sup>2</sup> )		h,s,r: $\chi$ -square = 8.33, df = 2, $P = 0.0155$ s,r: $\chi$ -square = 5.6907, df = 1, $P = 0.0171$										

EP = Eppelsheim, HO = Höwenegg. Mesowear variables: l = low, h = high, s = sharp, r = round, b = blunt; %l = percent low occlusal relief, %h = percent high occlusal relief, %s = percent sharp cusps, %r = percent rounded cusps, %b = percent blunt cusps; model = reference tooth positions investigated; four-tooth model = P<sup>4</sup>-M<sup>3</sup> (after Kaiser and Solounias, 2003, in press), one-tooth model = M<sup>2</sup> (after Fortelius and Solounias, 2000).

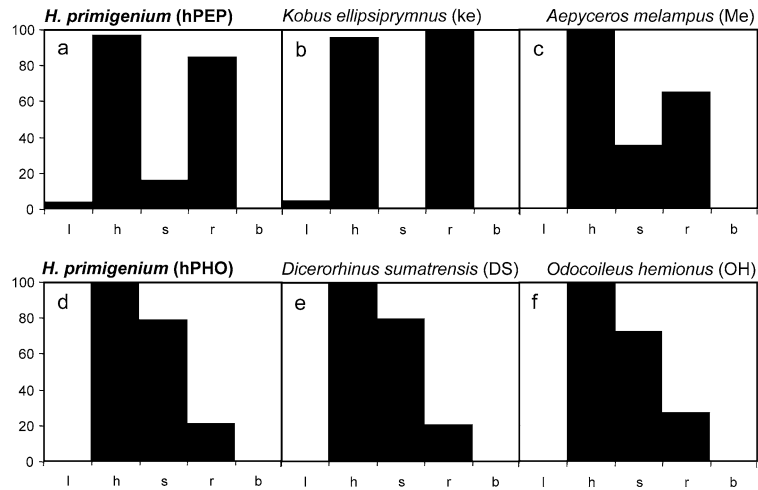


Fig. 4. Histograms of mesowear variables % low (l), % high (h), % sharp (s), % round (r) and % blunt (b). Histograms of *Hippotherium primigenium* are based on the values given in Table 4 (four-tooth model): Comparative histograms based on published data by Fortelius and Solounias (2000). (a) *Hippotherium primigenium* (Eppelsheim), (b) grazer *Kobus ellipsiprymnus* (common waterbuck), (c) hypsodont abrasion-dominated mixed feeder *Aepyceros melampus* (impala), (d) *H. primigenium* (Höwenegg), (e) browser *Dicerorhinus sumatrensis* (Sumatra rhinoceros), (f) browser *Odocoileus hemionus* (mule deer).

#### 4. Results

In all of the 20 upper cheek tooth specimens screened for microwear features at the cusps apices, microwear was still preserved in the Eppelsheim and the Höwenegg specimens investigated (Fig. 3).

##### 4.1. Frequency of mesowear variables

The frequency of mesowear variables scored is shown in Table 4 and Fig. 4. In the four-tooth model and in the one-tooth model, high occlusal reliefs prevail in both populations. In the HO-population, 100% of the specimens have high reliefs, in the EP-population, 3% are low in the four-tooth model. Cusp shape frequencies, however, are different. While no blunt cusps are recorded in both populations, major differences are observed in the frequencies of sharp and round cusps. There are 16% sharp cusps in the EP-population (Fig. 4a) and 79% in the HO-population (four-tooth model, Fig. 4d) and 0% in the EP-population versus 70% in the HO-population (one-tooth model, Table 4). If absolute counts of mesowear variables are tested for significance

of differences observed in the distribution pattern, all the observed patterns in the four-tooth model are highly significant. Less significance is achieved in the one-tooth model. Because no individuals were scored 'blunt', this mesowear variable was excluded from statistical analysis. If sharp cusps are tested versus round cusps, the *P*-value, which gives the probability that patterns observed are not different at an error probability of 0.05% is < 0.0001 (four-tooth model). This also applies if high occlusal relief is tested together with sharp and round cusps. If occlusal relief is tested independently, however, no significant difference is observed in the pattern. Taken together, the sum of all mesowear variables and the cusp shape variables alone in the four-tooth model provide good evidence that the trophic regimes of the two populations were different. In the one-tooth model, however, which incorporates only seven (EP) and 10 (HO) tooth specimens, respectively, the level of significance is much less meaningful.

##### 4.2. Cluster analysis

If all recent comparison species (Table 3) are employed in the four-tooth model (Fig. 5 and

Table 5  
Linkage pattern of cluster analysis Fig. 5 (all recent comparison species, four-tooth model)

Cluster containing species 1	Cluster containing species 2	Joined at distance	Number of species in new cluster
RS	AA	0.0	2
Ru	DS	0.0	2
Ta	Me	0.1	2
Rf	Tr	0.6	2
Ts	To	0.6	2
hP (HO)	Ru	0.6	3
OJ	OV	0.8	2
Oc	Gg	1.1	2
Ma	GC	1.2	2
Cl	EI	1.6	2
Lv	BE	1.6	2
Ap	he	1.7	2
Ts	Cc	2.1	3
OL	Ma	2.3	3
ke	TT	2.3	2
OJ	AM	2.4	3
Lg	Cl	2.5	3
LW	Ta	2.6	3
Rf	Ap	2.6	4
Bt	Lv	3.2	3
RS	DB	3.4	3
OH	OL	3.5	4
hP (EP)	Oo	3.6	2
Ts	Ca	4.1	4
Oc	Gt	4.2	3
hn	al	4.2	2
Sc	ke	4.4	3
LW	Lg	4.5	6
Cu	rr	4.7	2
OH	hp (HO)	5.4	7
Bt	Ts	5.9	7
Oc	Om	6.4	4
Tq	LW	6.5	7
Ti	Ci	6.5	2
eg	eb	7.0	2
ct	ab	7.1	2
OJ	RS	7.2	6
Cd	Ax	7.6	2
Rf	Cu	9.1	6
Sc	Rf	10.1	9
Oc	Ti	11.2	6
hP (EP)	Tq	11.4	9
Sc	hn	12.8	11
Bt	Oc	14.3	13
dl	eg	14.5	3
ct	Cd	14.8	4
hP (OH)	OJ	16.4	13
cs	dl	20.0	4
Sc	hp (EP)	23.7	20
Bt	OH	33.7	26
cs	bb	34.8	5
ct	Sc	34.9	24
St	Bt	41.6	27
ct	St	63.3	51
cs	ct	92.0	56

For abbreviations of species names see Table 3.

Table 5), *Hippotherium primigenium* from Eppelsheim (hP (EP)) is joined at a normalized Euclidean distance (NED) (root-mean-squared difference) of 24 with numerous mixed feeders like *Cervus unicolor* (Cu) and *Aepyceros melampus* (Me) and grazers including *Hippotragus niger* (hn), *Alcelaphus lichtensteini* (al) and *Kobus ellipsiprymnus* (ke). If only the 27 ‘typical’ recent comparison taxa are analyzed (Fig. 6 and Table 6), the EP sample classifies next to the grazers *Kobus ellipsiprymnus* (ke), *Redunca redunca* (rr), *Hippotragus equinus* (he), and *Hippotragus niger* (hn) in

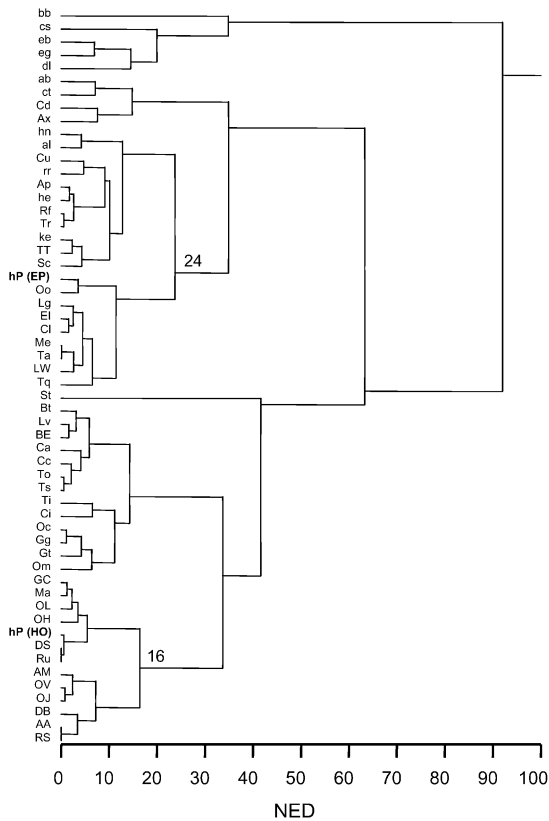


Fig. 5. Hierarchical cluster diagram based on the reference tooth positions P<sup>4</sup>–M<sup>3</sup> according to the ‘extended’ mesowear method (Kaiser and Solounias, 2003, in press). The mesowear features are percent high occlusal relief, percent sharp cusps and percent blunt cusps. Symbols as in Table 3. UPPER CASE = BROWSER, lower case = grazer, Mixed case (Capital first) = Mixed-feeder, mixed Case (lower First) = fossil species. Numbers at branching point indicate distance. Clusters based on all recent comparison species included in this study.

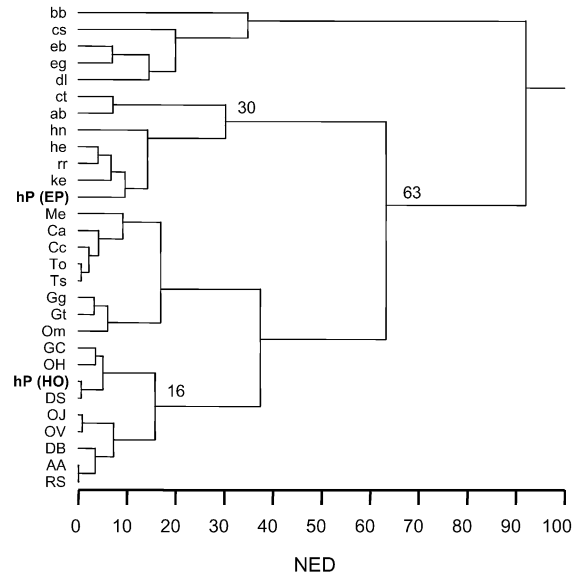


Fig. 6. Hierarchical cluster diagram based on the reference tooth positions P<sup>4</sup>–M<sup>3</sup> according to the ‘extended’ mesowear method (Kaiser and Solounias, 2003, in press). The mesowear features are percent high occlusal relief, percent sharp cusps and percent blunt cusps. Symbols as in Table 3, UPPER CASE = BROWSER, lower case = grazer, Mixed case (Capital first) = Mixed-feeder, mixed Case (lower First) = fossil species. Numbers at branching point indicate distance. Clusters based on a set of ‘typical’ recent species after Fortelius and Solounias (2000).

a subcluster of NED = 30 together with two more grazers exclusively. At the level of NED = 63, this cluster is joined with the eight mixed feeders and eight browsers in this comparison. In the one-tooth model, the classification varies only slightly (Fig. 8).

Including all recent comparison species in the four-tooth model (Fig. 5 and Table 5), *H. primigenium* from the Höwenegg (hP (HO)) classifies together with 10 browsers and two mixed feeders in a cluster of NED = 16. The species classifying closest are the browser *Dicerorhinus sumatrensis* (DS) and the mixed feeder *Rhinoceros unicornis* (Ru). If only ‘typical’ recent comparison taxa are analyzed (Fig. 6 and Table 6), the Höwenegg population is joined together with all the browsers of this group in a subcluster of NED = 16. It is linked closest to *Dicerorhinus sumatrensis* (DS), *Odocoileus hemionus* (OH) and *Giraffa camelopardalis* (GC). In the one-tooth model (Fig. 7, 8),

*Odocoileus hemionus* (OH) is the recent species linked closest.

## 5. Discussion

### 5.1. The possible influence of fluvial transport on the mesowear signal

Due to the higher-energy depositional environment at Eppelsheim, the influence of fluvial abrasion may be more pronounced there than in the Höwenegg assemblage. These taphonomic effects need to be considered as a potential agent obliterating mesowear; however, no studies of post-mortem sediment abrasion have been undertaken either in the Dinotheriensande, nor at the Höwenegg. Undoubtedly extensive sediment abra-

sion would round any prominence of specimens and therefore particularly affects the apices of tooth cusps. The sharpness of cusp apices, however, is one of the mesowear variables (cusp shape). Rounding by river transport therefore turns sharp cusps into round cusps, then round cusps into blunt, and finally high reliefs into low reliefs. Regarding the mesowear signal, fluvial transport therefore is expected to cause a gradual shift of the mesowear signal towards the apparent ‘grazing edge’ of the spectrum. In the Höwenegg assemblage no influence of sediment abrasion is expected. In the Eppelsheim sample, however, abrasion may have played a role in the taphonomic history (Fig. 2a). Because sediment abrasion affects prominence of sediment inclusions more than depressions, cusp tip apices are the most abrasion-sensitive parts of a hipparion cheek

Table 6  
Linkage pattern of cluster analysis Fig. 6 (typical recent comparison species, four-tooth model)

Cluster containing species 1	Cluster containing species 2	Joined at distance	Number of species in new cluster
RS	AA	0.0	2
Ts	To	0.6	2
hP (HO)	DS	0.6	2
OJ	OV	0.8	2
Ts	Cc	2.1	3
Gt	Gg	3.2	2
RS	DB	3.4	3
OH	GC	3.5	2
rr	he	4.0	2
Ts	Ca	4.1	4
OH	hp (HO)	5.0	4
Gt	Om	6.0	3
ke	rr	6.7	3
eg	eb	7.0	2
ct	ab	7.1	2
RS	OJ	7.2	5
Ts	Me	9.1	5
hP (EP)	ke	9.6	4
hP (EP)	hn	14.2	5
dl	eg	14.5	3
OH	RS	15.8	9
Ts	Gt	17.0	8
cs	dl	20.0	4
hP (EP)	ct	30.2	7
cs	bb	34.8	5
Ts	OH	37.4	17
hP (EP)	Ts	63.3	24
cs	hp (EP)	92.0	29

For abbreviations of species names see Table 3.

tooth occlusal surface. If abrasion took place to a certain extent, microwear striations and pits on the enamel surface should have been removed at the cusp tips first, but remain preserved at the valleys in between. On the other hand, the preservation of those features would be strong evidence for negligible abrasion on microwear, and consequently also on the mesowear signal. The fact that no evidence for the obliteration of microwear features is found in either sample leads to the conclusion that fluvial transport did not affect the Eppelsheim sample to an extent changing mesowear. The two dental samples can therefore be compared using the mesowear method

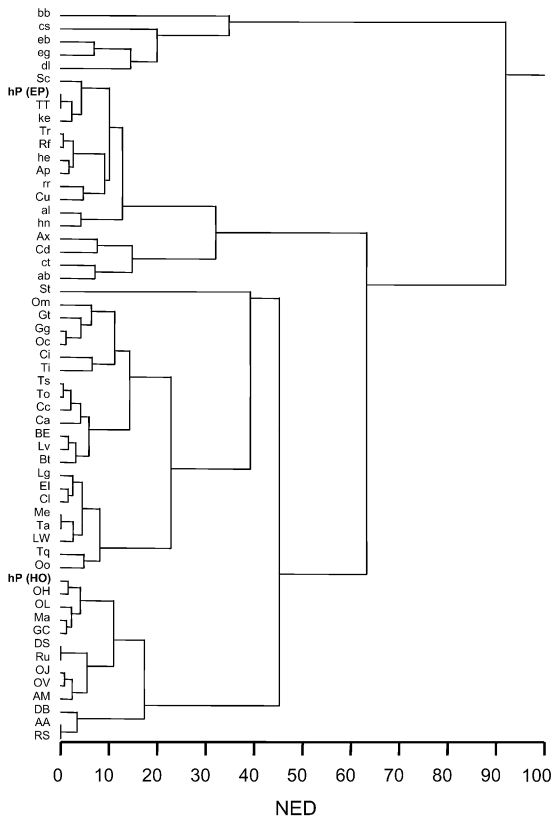


Fig. 7. Hierarchical cluster diagram based on the reference tooth position  $M^2$  according to Fortelius and Solounias (2000). The mesowear features are percent high occlusal relief, percent sharp cusps and percent blunt cusps. Symbols as in Table 3, UPPER CASE = BROWSER, lower case = grazer, Mixed case (Capital first) = Mixed-feeder, mixed Case (lower First) = fossil species. Clusters based on all recent comparison species included in this study.

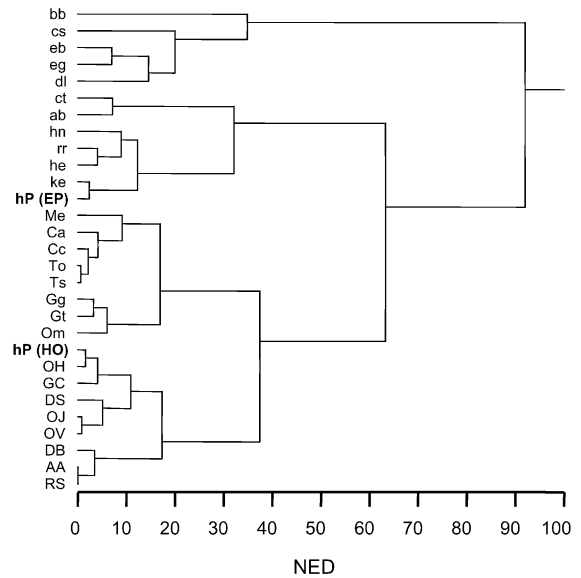


Fig. 8. Hierarchical cluster diagram based on the reference tooth position  $M^2$  according to Fortelius and Solounias (2000). The mesowear features are percent high occlusal relief, percent sharp cusps and percent blunt cusps. Symbols as in Table 3, UPPER CASE = BROWSER, lower case = grazer, Mixed case (Capital first) = Mixed-feeder, mixed Case (lower First) = fossil species. Clusters based on a set of 'typical' recent species after Fortelius and Solounias (2000).

without having to consider different taphonomic biases.

### 5.2. The trophic reference taxa

Based on the four-tooth model, the common waterbuck (*Kobus ellipsiprymnus*), is discussed as the trophic analog of the Eppelsheim population of *Hippotherium primigenium*. Waterbucks frequent reed beds and shrubby growth and also forage into woodlands (Nowak, 1999). According to Kingdon (1982) the major sources of food are medium and short grasses like *Andropogon*, *Brachiaria*, *Cenchrus*, *Chloris*, *Cynodon*, *Cyperaceae*, *Cymbopogon*, *Dichrostachys*, *Digitaria*, *Heteropogon*, *Hyparrhinia* and *Panicum* species, reeds and rushes (*Phragmites* and *Typha*). To a lesser extent browse like leaves and fruit are eaten (Walther, 1988; Kingdon, 1982). The prevailing dietary regime of the Eppelsheim assem-



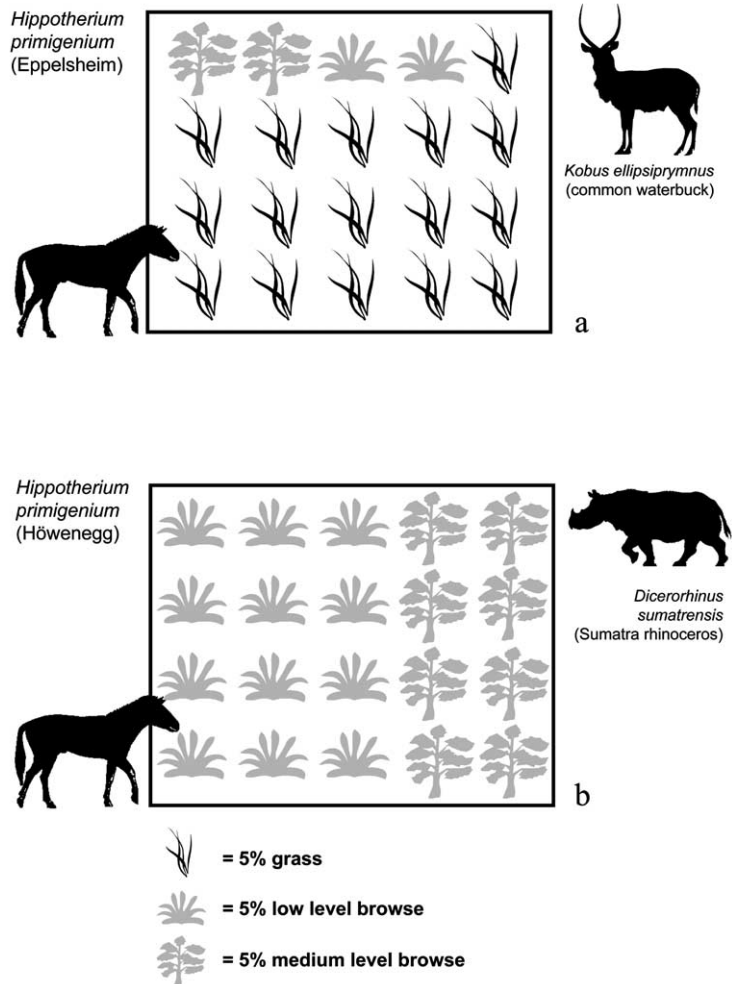


Fig. 9. The trophic regimes of the recent reference taxa. (a) *Kobus ellipsiprymnus*, the tropic reference taxon of the Eppelsheim population of *Hippotherium primigenium*, frequents reed beds and shrubby growth within the reach of water and forages into woodlands. The major source of food is grass and to a lesser extent also leaves. (b) *Dicerorhinus sumatrensis*, the trophic reference of the Höwenegg population of *H. primigenium*, inhabits both tropical rain forests and mountain moss forests. The major food sources are young saplings, fruit, leaves, twigs, and bark.

blage of *H. primigenium* is therefore considered equivalent to that of *K. ellipsiprymnus*. In this, the Eppelsheim population would appear to incorporate considerable amounts of graze in their diet. A grazing microwear signal has also been reported for a few specimens of the Middle–Late Miocene North American hipparions *Cormohipparion goorisi*, *C. quinni* and *C. occidentale* (Hayek et al., 1992) and for a single premolar of *Hipparion* sp. from Samos, Greece (Caprini, 1998).

Kaiser (2002) has documented that the enamel ridge alignment in the dentition of *C. occidentale* is highly optimized in showing maxima at 75–85° towards the chewing direction. The same optimization pattern is found in grazing extant ruminants (Kaiser, submitted). *H. primigenium*, which together with *C. occidentale* stands close to the base of a 10 Myr lasting radiation of hipparionine horses in the New World, is therefore expected to profit from this pre-adaptation in being capable

of coping with graze depending on the availability of food sources in the habitat.

The trophic reference taxon of the Höwenegg population, the Sumatran rhinoceros (*Dicerorhinus sumatrensis*), is an inhabitant of mainly hilly country near the water. It inhabits both tropical rain forests and mountain moss forests. The major food sources are young saplings, fruit, leaves, twigs, and bark (Nowak, 1999). For the Höwenegg population, therefore, a diet is suggested which, analogous to the diet of the Sumatra rhinoceros, predominantly consists of foliage, young shoots, herbs and buds (Fig. 9b).

### 5.3. The trophic spectrum at opportunistic food selection

The trophic preference of mammals with herbivorous adaptations is rarely very specific. Only few taxa are known to be almost exclusively dependent on a single taxon of food plants. *Ailuropoda melanoleuca*, the big panda, depends on bamboo (Schaller, 1988) and *Phascolarctus cinereus*, the koala, has a trophic adaptation that depends on foliage and bark of the about 20 *Eucalyptus* species (Moeller, 1988). These taxa are therefore examples of a particularly narrow trophic spectrum. Other taxa, among which are the majority of recent herbivores including the genus *Equus*, however, show a broader opportunistic strategy of food selection (e.g. Ansell, 1960; Darling, 1960; Lamprey, 1963; Roeder, 1999; Smuts, 1972, 1975; Ziccardi, 1970).

#### 5.3.1. The trophic spectrum of recent equids

Generally, modern *Equus* is regarded as a dedicated grazer. The actual food spectrum, however, is quite different and much more diverse in the individual *Equus* species investigated for trophic preferences, and by far does not only consist of grass. For *Equus burchelli*, Smuts (1972, 1975) mentions over 65 species of plants, among which are 50 species of grass, but also nine taxa of trees and bushes. Darling (1960) and Ansell (1960) record 'browse' as a source of food. Large parts of the vegetation accessible are taken as food by *Equus (Hippotigris) zebra hartmannae*. Observations by Roeder (1999) have shown that during

drought periods 'browse' makes up a large portion of the food taken by *E. zebra zebra* in Namibia. Generally, this taxon seems to prefer nutritious, 'green' plant parts in its southern populations and shows a considerable plasticity in food selection, which is widely dependent upon the food items available in the habitat. Ziccardi (1970) provides information that *Equus (Asinus) asinus* uses a large part of the vegetation as food available in the scarce habitats of these animals.

The variety of food items ingested by recent *Equus* under given habitat conditions indicates that recent equids are not specialized grazers, but that grass may serve as the only source of food, if no other vegetation is available. The diet of *Equus* therefore should mirror the food availability in a given habitat with all plant matter taken as food which is within the trophic spectrum of the taxon.

#### 5.3.2. Reconstructing habitat conditions based on the trophic signal of a single taxon

If several populations from different habitat types are investigated, the trophic signal of the Equidae not only indicates the trophic spectrum of a given equid taxon, but also provides information on the availability of food items in a given habitat. This in turn provides evidence of the structure of paleohabitats, the biotic and abiotic parameters influencing plant growth and diversity. It should therefore be possible to infer habitats of extinct mammals from differential trophic signals of a single mammal species inhabiting the habitats compared. This approach of reconstructing habitat parameters is justified if the following conditions are met:

(1) The same taxon of herbivorous mammal is present in two habitats to be compared and may serve as two reference populations.

(2) There is no reason to expect that the trophic spectrum of the two populations was different. This condition is most likely to be met if the populations are close in time, which makes differential adaptations less likely.

(3) The seasonality of the climate was similar in the paleohabitats compared. This demand is required to ensure that non-equalities in the avail-

ability of food plants caused by seasonality have a uniform influence on the trophic signal of the reference populations.

5.3.2.1. *The trophic spectrum of Hippotherium primigenium as an instrument in reconstructing differential habitat conditions:* The conditions mentioned above are met for the two Vallesian faunas from Eppelsheim and Höwenegg. Both localities have yielded *H. primigenium*, and both are dated in the MN9 zone of mammal stratigraphy, with less than 0.2 Myr difference in age (Woodburne et al., 1996b). This makes it unlikely that differences in trophic preference are the result of specific adaptive processes of the individual populations. Trophic differences observed should therefore reflect the ecological spectrum of *H. primigenium*, which, based on the trophic preferences of the analog taxa identified in this study, is expected to be rather large, extending from ‘moderate grazing’ (Eppelsheim) to dedicated ‘browsing’ (Höwenegg).

If this argument is followed, and the trophic signal of *H. primigenium* is interpreted as an ecological signal reflecting properties of the habitat, the paleohabitat of the Dinotheriensande would be recognized as representing at least seasonally extended grassy areas. This is not really surprising, as the Dinotheriensande complex is a fluvial environment bordered by an Ulmus–Salix type aue vegetation, as indicated by the associated leaf flora (Meller, 1989). Recent Central European aue forests have a herb layer, with extended components of abrasive C3 grasses such as e.g. *Agrostis* and *Phalaris*. The fact that the leaf flora of Sprendlingen does not preserve members of the herb layer is considered a taphonomic effect intrinsic to deciduous forest leaf floras, and does not mean that no graminiflora existed in the Dinotheriensande habitat.

The graminiflora intrinsic to aue vegetations is therefore considered a readily available grazing ground for the Eppelsheim hipparions (Fig. 2a). This habitat condition would be well reflected by the trophic signal of *Hippotherium primigenium*, which is not the signal of a ‘hyper-grazer’, such as e.g. the recent *Equus burchelli*, which takes large amounts of highly abrasive dry grasses

(Lamprey, 1963; Vesey-FitzGerald, 1960). *Kobus ellipsiprymnus*, the reference taxon for the Eppelsheim population, is actually a grazer bound to flooding areas near the water, with plenty of grass and reed vegetation available.

The condition suggested for the Eppelsheim paleohabitat, however, is not necessarily indicative of the ecological situation during the Upper Miocene of large parts of Central Europe, where grasslands have not been extensively developed due to the humid climate in the Vallesian (Bernor et al., 1988). It rather reflects a local condition, which allows reconstructing a circumscribed environment as the one represented by the Dinotheriensande.

At Höwenegg, however, the hipparions must have had sufficient supply of other foods, making grass less important in the trophic regime. Since the influence of abrasive food items does not contribute to the mesowear signal of this population, it is likely that abrasive food such as e.g. grass was not abundant. Therefore, it is likely that within the foraging range of the Höwenegg hipparion population, the center of which is marked by the postulated Höwenegg Lake (Tobien, 1986; Woodburne et al., 1996b), open habitats did not exist (Fig. 2b). The paleohabitat of the Höwenegg was most likely part of the subtropical mesophytic forests that covered large parts of Central- and Western Europe, Central Asia and southern China during the Vallesian period (Bernor et al., 1988). This finding supports earlier evidence from the fossil flora from Höwenegg (Gregor, 1982) as well as from the fauna, as pointed out by the presence of the rhinocerotids *Aceratherium incisivum* (Kaup, 1829) and *A. simorreense* (Lartet, 1851) that, according to Guerin (1981), preferred wooded habitats in the proximity to swamps and lakes. Also, the cervids *Muntiacinarum* genus and *Miotragocerus pannoniae* support this habitat reconstruction because, like their closest living relatives, they were probably forest denizens. At various European localities from the Upper Miocene, both taxa are associated with corresponding floral remains (Tobien, 1986).

### 5.3.3. Conclusion

In both contemporaneous populations of *Hip-*

*pothorium primigenium* investigated, the mesowear signal leads to the identification of a recent reference taxon, the trophic preferences of which are consistent with the proposed food availability intrinsic to habitat conditions indicated independently by faunal, floral and taphonomic evidence. This points to the tremendous potential the extended mesowear method has in gaining evidence on the structure of local paleohabitats. The findings of this study, however, also remind us to take precautions in interpreting the mesowear signal of a single population (and probably any trophic signal, independently of the method it is based upon) as a specific trophic adaptation, in the sense of a dedicated specialization within the ecological range of a paleocommunity. However, if several populations from different ecological contexts are compared, the trophic spectrum of individual taxa needs to be known before specific inference of the ecological role of a species can be gained. The trophic spectrum of *H. primigenium* manifested in the wide span of the trophic classifications in the two populations of *H. primigenium* points to a problem little emphasized so far. In this span, *H. primigenium* would appear as a generalist, and it would be interesting to investigate the trophic spectrum of contemporaneous taxa from the Rhinocerotidae and the ruminants.

*H. primigenium* is one of the first hipparions reaching Europe in the Upper Miocene and therefore stands close to the base of a 10 Myr lasting radiation of hipparionine horses in the New World (Woodburne et al., 1996a). This finally resulted in a wide range of trophical and locomotor adaptations. Besides dental adaptations (Kaiser, 2002), the large ecological spectrum of *H. primigenium* may therefore well be one of the pre-adaptations crucial for the dispersal and radiation of the group further on. The Höwenegg population of *H. primigenium*, which has been shown to display the trophic signal of the widespread mesophytic forest vegetation prevailing in large parts of Europe and Asia during the Vallesian time, will therefore serve as a reference population for these habitat conditions in further comparisons of hipparion populations from Central and Eastern Europe and Eurasia (Bernor et al., in press).

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