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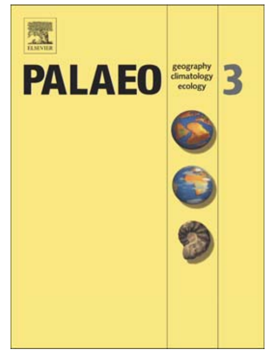

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Ungulate feeding ecology and Middle Pleistocene paleoenvironments at Hundsheim and Deutsch-Altenburg 1 (eastern Austria)

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Abstract

The purpose of this study is to analyze the dietary traits in the ungulate communities from two middle Pleistocene localities in eastern Austria, Deutsch-Altenburg 1 and Hundsheim, and to revise the paleoecological reconstructions at each site using tooth wear analyzes (mesowear and microwear). The data will also be used to test for intra- and inter-site differences and analyze resource partitioning among ungulates. Intra-site comparisons show significant differences at the two localities and reveal the use of different resources for the various ungulates studied. This suggests the existence of dietary partitioning and niche segregation that would not be detected using traditional morphological proxies. The local environment at the two sites is characterized by the availability of both open and forested habitats. This study indicates the presence of mixed environmental conditions which is a different conclusion from previous paleoenvironmental reconstructions.

Keywords: Microwear, mesowear, diet partitioning, ungulate community.

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1. Introduction

Fossil ungulates are commonly employed as proxies for reconstructing past environmental conditions at paleontological or archaeological sites by following the uniformitarianism principle. In the past decades, proxies such as stable isotopes and dental wear analyses improved the resolution of the methods based on morphological proxies (e.g., Cerling et al., 1997; Kaiser and Rössner, 2007; MacFadden and Cerling, 1994; Rivals et al., 2008; Rivals et al., 2009; Semprebon et al., 2004a). During the Quaternary, in particular, the response of large mammals (morphological change or changes in the faunal composition) to climatic and environmental changes is usually synchronous but it may also be asynchronous, depending of the quality and resolution of the fossil record. The lack of temporal synchronicity between changes in tooth morphology (e.g. tooth crown height) and tooth wear (microwear or mesowear) may be explained by the fact that dietary changes are more labile than morphologic changes (Feranec, 2007a).

The objective of this study is to analyze the dietary traits in the ungulate communities from two middle Pleistocene localities in eastern Austria, Deutsch-Altenburg 1 and Hundsheim and to revise the paleoecological reconstructions at each site using tooth wear analyzes (mesowear and microwear). The data will also be used to test for intra- and inter-sites differences and to analyze resource partitioning among ungulates. The aim is to test the hypothesis that differences exist between species occurring at the two localities which are consistent with the paleoenvironmental reconstruction.

2. Material and methods

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Material was analyzed from two middle Pleistocene localities from eastern Austria: Deutsch-Altenburg 1 and Hundsheim. The material is housed in the collections of vertebrate paleontology (Department of Geology and Paleontology) at the Naturhistorisches Museum in Vienna.

Deutsch-Altenburg 1 was discovered during the mining activities in the Hainburg Hills in the Hollitzer Baustoffwerke area (Frank and Rabeder, 1997a). The fossil mammal remains collected between 1911 and 1912 and described by Freudenberg (1914) were revised by Nagel and Rabeder (1997). The fauna includes *Ursus deningeri*, *Meles meles*, *Panthera spelaea*, *Canis mosbachensis*, Proboscidea indet., *Capreolus capreolus*, *Cervus elaphus*, *Bison schoetensacki*, *Stephanorhinus hundsheimensis*, and *Equus ferus mosbachensis*. The evolutionary stages of *Ursus*, *Canis*, *Bison* and *Equus* indicate a Middle Pleistocene age for this fauna (Nagel and Rabeder, 1997).

Hundsheim was discovered during the mining activities in the karstic Hainburg Hills between Hainburg, Bad Deutsch-Altenburg and Hundsheim in 1900 (Toula, 1901, 1902, 1907; Wüst, 1907; Freudenberg, 1908, 1914) and subsequently excavated at irregular intervals until 1960 (Frank and Rabeder, 1997b). The Hundsheim fissure, which does not exist anymore, was located on southern slopes of Hainburg Hills at the north-west of Hundsheim, ca. 260 m a.s.l. In addition to other fossils, the fissure of Hundsheim yielded a rich micromammal fauna (Kormos, 1937; Rabeder, 1972, 1981), which allowed dating the excavated taphocenosis in the earliest middle Pleistocene, particularly in the MNQ-zone 22 (sensu Guérin, 1982). Hundsheim deposits are older than those from Deutsch-Altenburg 1 (Nagel and Rabeder, 1997).

At each locality, all the available material was sampled. At Deutsch-Altenburg 1, this includes Proboscidea indet. (N=3), *Equus ferus mosbachensis* (N=13), *Cervus elaphus* (N=3), *Capreolus capreolus* (N=5), and *Bison schoetensacki* (N=5). At Hundsheim, this

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includes *Stephanorhinus hundsheimensis* (N=5), *Cervus elaphus* (N=5), *Capreolus capreolus* (N=6), *Bison schoetensacki* (N=17), and *Hemitragus bonali* (N=22).

2.1. Tooth mesowear

Mesowear analysis, first introduced by Fortelius and Solounias (2000), is a method of categorizing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices in ways that are correlated with the relative amounts of attritive and abrasive dental wear. Mesowear is scored macroscopically from the buccal side of upper molars, preferably the paracone of M2 (Fortelius and Solounias, 2000). Among taxa with the appropriate masticatory apparatus, a diet with low levels of abrasion (such as the browsing diet of the moose) maintains sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass and/or a high rate of soil or dust particle ingestion (such as the coarse grazing diets of African zebra) results in more rounded and blunted buccal cusp apices. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices are omitted from mesowear analyses. Cusp sharpness is sensitive to ontogenetic age among young individuals (who have not yet developed substantial wear facets) and among dentally senescent individuals. However, for intermediate age groups, which typically include the majority of individuals in a fossil collection, mesowear was found to be less sensitive to age and more strongly related to diet (Rivals et al., 2007a). In this study, the standardized method (mesowear "ruler") introduced by Mihlbachler et al. (2011) is employed. The method is based on seven modern horse cusps (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to

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completely blunt with no relief (stage 6). Using the mesowear ruler as a reference, fossil cusps equal to or sharper and higher in relief than reference cusp 0 were assigned a 0. Cusps that morphologically are intermediate between reference cusps 0 and reference cusp 1, or equal to reference cusp 1 were assigned a 1, and so forth. The average value of the mesowear data from a single sample of fossil dentitions is the "mesowear score" (Mihlbachler et al., 2011).

2.2. Tooth microwear

All available upper and lower second molars (M2 or m2) of dentally adult individuals, whether isolated or in tooth rows were sampled following the methodology of Solounias and Semprebon (2002). The occlusal surface of each tooth was molded using polyvinylsiloxane dental impression material. Each mold was cast with clear epoxy resin. Microwear analysis was performed using low-magnification stereomicroscopy following methods outlined by Solounias and Semprebon (2002), and Semprebon et al. (2004b). High-resolution epoxy casts of the teeth were examined at 35x magnification using a Leica MZ16 stereomicroscope. Light was shone onto the surface of the casts (by adjusting the angle of the incident light beam and its intensity). Examination of microwear was done on the enamel band of the paracone of the upper second molar or alternatively on the protoconid of the lower second molar. Microwear features are identified, counted and classified on the basis of differential light refraction properties as outlined by Solounias and Semprebon (2002) and Semprebon et al. (2004b) and assigned to four categories: small pits, large pits, fine (narrow) scratches and coarse (wide) scratches. Counts of microwear features were made on a standard 0.16 mm^2 square area on each tooth. Using modern species of known diets, counts of the numbers

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of pits and scratches in the counting area at a constant magnification of 35x are capable of discriminating three main recognized dietary categories within the herbivore dietary continuum, fruit browser, leaf browser, and grazer (Solounias and Semprebon, 2002; Semprebon et al., 2004b). The presence or absence of large pits, gouges and cross scratches (i.e., those oriented somewhat perpendicularly to the majority of scratches) within the 0.16 mm^2 area was also reported. In addition, scratch textures were assessed as being either fine, coarse, or hypercoarse or a mixture of fine and coarse scratches per tooth surface. Scratch textures were converted into a scratch width score (SWS) to simplify representation of the data by giving a score of '0' to teeth with predominantly fine scratches per tooth surface, '1' to those with a mixture of fine and coarse types of textures, and '2' to those with predominantly coarse scratches. Individual scores for a sample were then averaged to get the scratch width score.

3. Results

3.1. Mesowear

Mesowear scores from Deutsch-Altenburg 1 and Hundsheim show a wide range of relative abrasiveness in the diet, from low abrasive diets in the cervids (*Cervus elaphus* and *Capreolus capreolus*) and the rhinoceros (*Stephanorhinus hundsheimensis*), to high abrasion in the horse (Table 1, Fig. 1). Bovids (*Bison schoetensacki* and *Hemitragus bonali*) have intermediate scores. The range covered by ungulate mesowear at Deutsch-Altenburg is greater than at Hundsheim due to the highly abrasive diet of the horse at Deutsch-Altenburg.

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When compared to their modern relatives, most of the fossil species have similar mesowear scores (Fig. 1). The only exception is *Stephanorhinus hundsheimensis* which has a mesowear score that is very different from the extant *Ceratotherium simun* or *Diceros bicornis*. The bison (*Bison schoetensacki*) from the two localities have mesowear scores more similar to the extant European bison (*Bison bonasus*) and the wood bison (*B. b. athabascae*) rather than to the plains bison (*B. b. bison*). Finally, the red deer samples (*Cervus elaphus*) are more similar to the European species than to the North American sample.

3.2. Microwear

Bivariate analysis of the average numbers of pits and scratches (Fig. 2A and B) and the scratch distribution (%0-17; Table 1) indicate that most of the ungulates from Deutsch-Altenburg 1 and Hundsheim were either mixed feeders or leaf browsers. Only the sample of Proboscidea indet. from Deutsch-Altenburg 1 displays a microwear pattern similar to the grazers with high number of scratches and low numbers of pits. Comparing species present at the two localities, the two cervids have the same dietary traits. *Capreolus capreolus* is a mixed feeder and *Cervus elaphus* is browsing at the two localities. The samples of *Bison schoetensacki*, on the contrary, show different dietary traits. The sample from Deutsch-Altenburg 1 has results consistent with browsing while the sample from Hundsheim has results consistent with mixed feeding. Considering that microwear provides a temporal snapshot of the diet, it is possible that the sample from Deutsch-Altenburg 1 results from a mortality event that occurred at a season when the species was browsing. It is interesting to observe that the sample from Hundsheim and, to a lesser extent the sample from Deutsch-Altenburg, are more similar to the extant

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European bison *Bison bonasus* rather than to the two sub-species from the Nearctic, *Bison bison bison* and *B. b. athabascae* (Fig. 3). The same observation is noted for *Cervus elaphus*. The two fossil samples from Austria are more similar to their European modern relatives than to the North American elk. As also observed through mesowear, the rhino, *Stephanorhinus hundsheimensis*, is not similar to the two extant comparative species.

The results from tooth microwear are consistent with those obtained through mesowear except for *Equus ferus*. Considering the temporal resolution differences of each proxy, the discrepancy between mesowear (grazing) and microwear (browsing) in that species would indicate a mixed feeding trait.

The comparison of scratch width score (SWS) among the species present at the two localities (*Bison schoetensacki*, *Cervus elaphus*, and *Capreolus capreolus*) shows a shift toward wider scratches (coarse scratches) from Hundsheim to Deutsch-Altenburg 1 (Fig. 3). Such similar and consistent shifts in the three species would seem to be related to a change in the diet. However, those differences are not significant for any of the three species (Table 2).

4. Discussion

Tooth mesowear on ungulates from Deutsch-Altenburg 1 and Hundsheim indicate a large diversity of abrasiveness in the diet. The cervids (*Cervus elaphus* and *Capreolus capreolus*) and the rhinoceros (*Stephanorhinus hundsheimensis*) fed on low abrasive items similar to those used by extant cervids in closed habitats. Conversely, the horse from Deutsch-Altenburg 1 (absent at Hundsheim) has the highest mesowear scores indicating high abrasion levels similar to the extant zebras (Table 1, Fig. 1). The bovids

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(*Bison schoetensacki* and *Hemitragus bonali*) are intermediate in terms of their mesowear and similar to extant mixed feeders or grass-dominated mixed feeders.

When comparing the species that are present at the two localities (*Bison schoetensacki, Cervus elaphus, Capreolus capreolus*) it appears that most of the mesowear and microwear variables do not show any significant differences (Table 2). This indicates that the dietary traits for those three species do not vary significantly at the two localities. The hypothesis tested is not supported by the data from Deutsch-Altenburg 1 and Hundsheim. However, intra-site comparisons show significant differences in tooth mesowear and microwear at the two localities (Table 2). Such differences reveal the use of different resources for the various species studied and suggests the existence of diet partitioning and niche segregation. The significant differences observed in tooth mesowear and microwear of the ungulate taxa of Deutsch-Altenburg 1 and Hundsheim reveal that it is possible to detect differences in resource use and niche partitioning among ungulate taxa using tooth wear as a proxy for dietary traits (Calandra et al., 2008; DeSantis et al., 2009; Feranec, 2007b; Kaiser, 2011; Rivals et al., 2010). This differential resource utilization is based on behavioral variation which would not be detected using the traditional morphological proxies (e.g., hypsodonty, premaxillary shape).

The tooth wear analysis of the ungulate communities at Deutsch-Altenburg 1 and Hundsheim indicates environments with both open and forested habitats available to ungulates; however Deutsch-Altenburg 1 appears to have been more open in terms of habitat than Hundsheim with the occurrence of a pure grazer (Proboscidea indet.) and to a lesser extent due to the presence of a mixed feeding horse. The paleoenvironmental reconstruction proposed for Hundsheim reports a dominance of open steppe (Frank and Rabeder, 1997b). Similarly, at Deutsch-Altenburg 1, a mostly steppic environment was

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proposed on the basis of the presence of bison, horse and rhinoceros (Frank and Rabeder, 1997a; Nagel and Rabeder, 1997). Hence, previous studies report mostly open steppic environments for the two localities. However, this tooth wear analysis reveals more browsing and mixed feeding dietary traits which suggest that the slopes of the Hainburg Hills, where the sites are located, were probably covered by mixed forests and surrounded by dry steppes. This interpretation is supported by recent results from a study of the fossil bird fauna from Hundsheim which belong to two basic ecological groups, a dominant group with species that inhabit mixed forests and one, in numeric minority, with inhabitants of open dry steppes (Mlíkovský, 2009). This indicates a more mixed environment than previous studies.

Differences reported here from previous interpretations may be related to the resolution of tooth wear methods that reflect the immediate dietary behaviour of the ungulate populations at each locality, thus indicating the local environmental conditions at each site during the accumulation of those assemblages.

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Figure captions

Figure 1. Mesowear scores based on the extant reference species from Fortelius and Solounias (2000) and the middle Pleistocene samples from Deutsch-Altenburg 1 and Hundsheim. Extant taxa are classified as leaf browsers (LB), mixed feeders (MF) and grazers (G). Mesowear score for extant species calculated from Fortelius and Solounias (2000): **Browsers**: AA = *Alces alces*, AM = *Antilocapra americana*, DB = *Diceros bicornis*, DS = *Dicerorhinus sumatrensis*, GC = *Giraffa camelopardalis*, LW = *Litocranius walleri*, OH = *Odocoileus hemionus*, OJ = *Okapia johnstoni*, OL = *Capreolus capreolus*, OV = *Odocoileus virginianus*, RS = *Rhinoceros sondaicus*, TE = *Tragelaphus euryceros*, TT = *Tragelaphus strepsiceros*; **Grazers**: ab = *Alcelaphus buselaphus*, al = *Sigmoceros lichtensteinii*, bb = *Bison bison*, cs = *Ceratotherium simum*, ct = *Connochaetes taurinus*, dl = *Damaliscus lunatus*, eg = *Equus grevyi*, eq = *Equus quagga*, he = *Hippotragus equinus*, hn = *Hippotragus niger*, ke = *Kobus ellipsiprymnus*, rr = *Redunca redunca*; **Mixed feeders**: Ax = *Axis axis*, Bt = *Budorcas taxicolor*, Ca = *Capricornis sumatraensis*, Cc = *Cervus elaphus canadensis*, Cd = *Cervus duvauceli*, Ci = *Capra ibex*, Cu = *Cervus unicolor*, Gg = *Gazella granti*, Gt = *Gazella thomsoni*, Hj = *Hemitragus jemlahicus*, Lv = *Lama vicugna*, Ma = *Antidorcas marsupialis*; Me = *Aepyceros melampus*; Oc = *Ovis canadensis*, Om = *Ovibos moschatus*, Oo = *Ourebia ourebi*, Op = *Ovis ammon poli*, Pc = *Procavia capensis*, Rf = *Redunca fulvorufula*, Rt = *Rangifer tarandus*, Ru = *Rhinoceros unicornis*, Sc = *Syncerus caffer*, St = *Saiga tatarica*, Ta = *Tragelaphus angasi*, Ti = *Tragelaphus imberbis*, To = *Taurotragus oryx*, Tq = *Tetracerus quadricornis*, Tr = *Boselaphus tragocamelus*. Abbreviations for the fossil species: *Equus ferus* (Ef), *Stephanorhinus*

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hundsheimensis (Sh), *Capreolus capreolus* (Cc), *Cervus elaphus* (Ce), *Bison schoetensacki* (Bs), *Hemitragus bonali* (Hb).

Figure 2. Bivariate diagram based on microwear signatures of extant reference species from Solounias and Semprebon (2002) and the ungulate samples from Deutsch-Altenburg 1 (A) and Hundsheim (B). Grey areas indicating Gaussian confidence ellipses (p = 0.95) on the centroid of the grazer/browser sample adjusted by sample size. Abbreviations: Proboscidea indet. (Pr), *Equus ferus* (Ef), *Stephanorhinus hundsheimensis* (Sh), *Capreolus capreolus* (Cc), *Cervus elaphus* (Ce), *Bison schoetensacki* (Bs), *Hemitragus bonali* (Hb).

Figure 3. Average number of scratches vs. Scratches Width Scores (SWS) for Deutsch-Altenburg 1 (black squares) and Hundsheim (grey squares) compared to their modern relatives (white squares). Abbreviations from Table 1. Dashed lines connect pairs of species from the two localities.

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Table 1. Mesowear and microwear summary data for the samples from Deutsch-Altenburg and Hundsheim. Abbreviations: MWS = mesowear score; NP = average number of pits; NS = average number of scratches; %LP = percentage of specimens with large pits; %XS = percentage of specimens with cross scratches; %G = percentage of specimens with gouges; SWS = scratches width score (from 0 = fine scratches only to 2 = coarse scratches only); %0-17 = percentage of specimens with between 0 and 17 scratches, and N/A = not applicable; Diet = Dietary category resulting from dental wear analysis; B = leaf browser; G = grazer; MF = mixed feeder. References for the modern relative species: (1) Fortelius and Solounias (2000), (2) Solounias and Semprebon (2002), (3) Rivals et al. (2010), (4) Rivals et al. (2007b), (5) this study.

		Mesowear		Microwear								
Species		N	MWS	N	NP	NS	%LP	%XS	%G	SWS	%0-17	Diet
Deutsch-Altenburg												
Proboscidea indet.	Pr	-	N/A	3	14.5	19.0	0.0	33.3	66.7	0.0	0.0	G
Equus ferus mosbachensis	Ef	12	4.5	13	29.5	15.6	23.1	0.0	15.4	1.2	76.9	MF
Cervus elaphus	Ce	3	1.7	3	24.3	10.5	66.7	0.0	33.3	1.7	100.0	B
Capreolus capreolus	Cc	2	1.0	5	39.9	16.8	20.0	0.0	20.0	1.2	40.0	MF
Bison schoetensacki	Bs	5	2.4	5	28.4	16.7	80.0	80.0	80.0	1.4	80.0	B
Hundsheim												
Stephanorhinus hundsheimensis	Sh	5	1.4	5	30.8	12.9	0.0	80.0	20.0	1.6	80.0	B
Cervus elaphus	Ce	5	1.6	5	19.8	14.1	20.0	60.0	0.0	1.0	100.0	B
Capreolus capreolus	Cc	6	0.5	6	23.2	18.0	0.0	0.0	0.0	0.8	33.3	MF
Bison schoetensacki	Bs	17	2.8	17	33.2	18.1	43.8	37.5	25.0	1.2	41.2	MF
Hemitragus bonali	Hb	22	2.5	22	20.4	18.1	13.6	18.2	9.1	1.1	40.9	MF
Modern relative species												
Ceratotherium simum (1, 3)	Cra	24	4.7	10	95.9	18.6	40.0	40.0	30.0	0.30	30.0	
Diceros bicornis (1,3)	Dbi	34	0.1	34	88.6	11.5	90.0	50.0	40.0	0.20	90.0	
Equus quagga (1, 2)	Eqq	121	4.7	51	11.5	21.7	49.0	60.0	52.9	1.10	15.7	
Equus grevyi (1, 2)	Eqg	29	4.5	11	7.9	26.1	63.6	66.7	54.5	1.33	9.1	
Cervus elaphus Europe (1, 2)	Ce-eu	33	1.7	28	13.3	13.4	0.3	0.3	0.4	1.46	89.3	
Cervus elaphus N. America (3)	Ce-na	19	1.1	28	18.6	30.6	42.9	96.4	21.4	0.36	10.7	
Capreolus capreolus (1, 2)	Cap	68	0.7	34	25.5	12.5	47.1	11.6	23.5	0.91	88.2	
Bison bison athabascae (4)	Bba	11	2.0	8	21.3	19.8	0.0	0.0	0.0	0.50	12.5	
Bison bison bison (1, 2)	Bbb	15	5.5	18	3.5	24.8	38.9	94.4	5.6	1.06	5.6	
Bison bonasus (5)	Bbo	7	3.1	11	21.3	19.7	72.7	18.2	45.5	1.09	18.2	
Hemitragus hylocrius (5)	Hhy	7	2.3	5	16.4	18.9	40.0	40.0	20.0	1.40	20.0	
Hemitragus jemlahicus (5)	Hje	19	1.9	15	26.6	19.0	46.7	26.7	26.7	1.07	26.7	

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Table 2. P values for non-parametric Mann-Whitney U test (for differences between two samples) and Kruskal-Wallis test (for tests with 3 or more samples). Bold indicates significant differences. Abbreviations see Table 1.

	MWS	NP	NS	SWS
inter-site comparisons				
Bison vs *Bison*	0.337	**0.020**	0.319	0.484
Cervus vs *Cervus*	1.000	0.134	0.074	0.075
Capreolus vs *Capreolus*	0.324	**0.008**	0.517	0.223
intra-site comparisons				
All Deutsch-Altenburg	**0.001**	**0.002**	**0.033**	
All Hundsheim	**0.000**	**0.000**	**0.002**	

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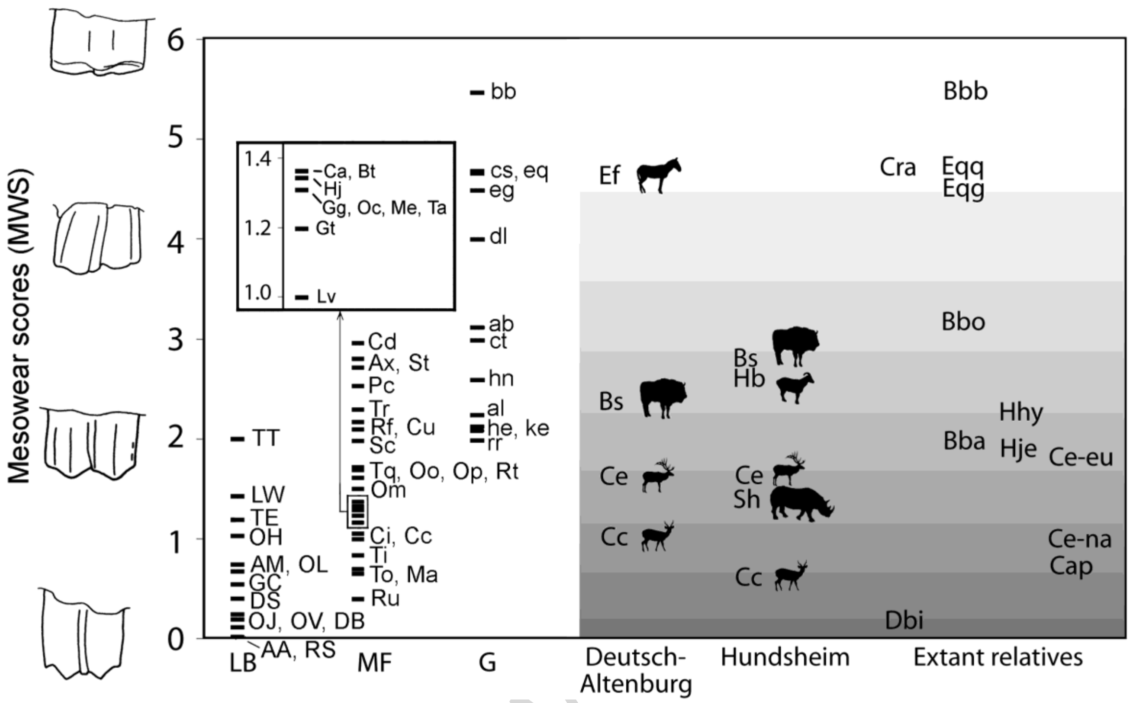

Figure 1

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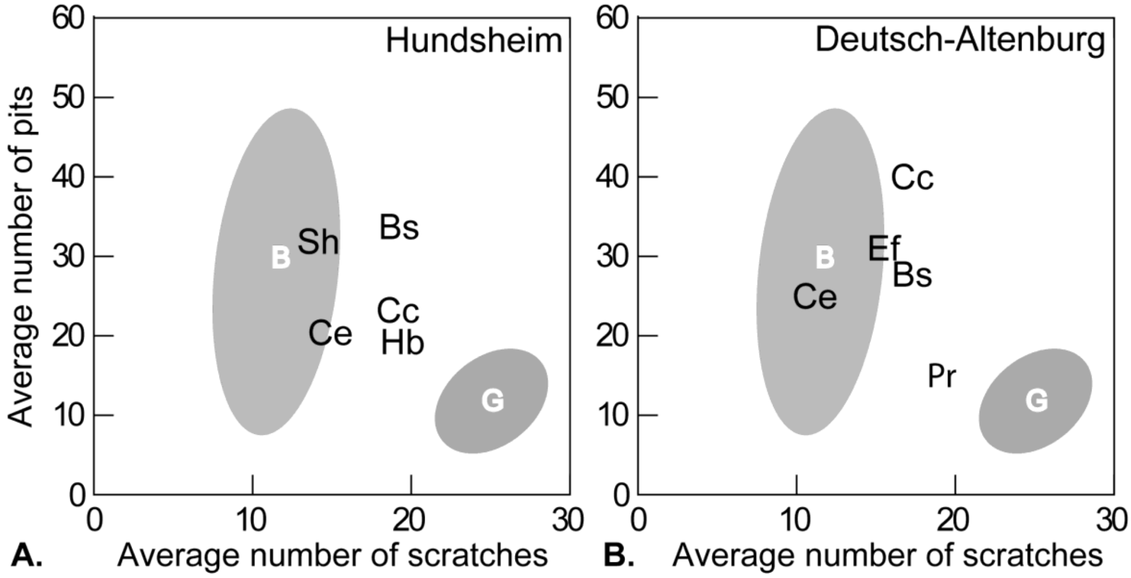

Figure 2

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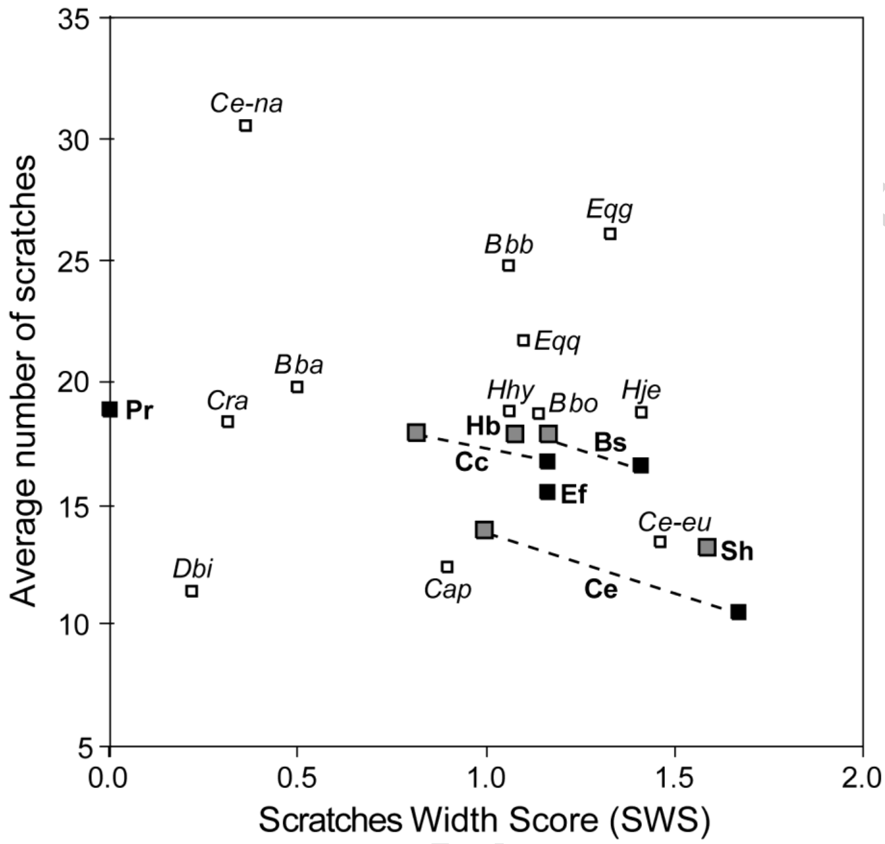

Figure 3

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Research highlights

> Analysis of ungulate dietary traits in two middle Pleistocene localities from Austria

> Revision of paleoenvironmental reconstructions using tooth mesowear and microwear

> Intra-site comparisons suggest diet partitioning and niche segregation among ungulates

> The local environment is characterized by mixed conditions (open and forested habitats)

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