

The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria)

13. Dental wear patterns of herbivorous ungulates as ecological indicators

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(With 2 figures and 4 tables)

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Abstract

The present study characterizes the ecological niches of equids and ruminants along with the environmental conditions that prevailed at the Atzelsdorf locality (Austria) in the early Vallesian. Dental micro- and meso-wear analyses were used to determine the feeding preferences of these ungulates. *Dorcatherium nauti* and *Micromeryx flourensianus* were browsers specialized in frugivory, whereas the bovid (either *Miotragocerus* or *Tethytragus*) was a leaf-eater. The two equids *Hippotherium* sp. and *Anchitherium aurelianense* were also browsers. The total absence of grazers in Atzelsdorf strongly supports the dominance of forested landscapes along the shores of Lake Pannon during Vallesian times. The results also emphasize the ecological plasticity of high-crowned hipparionines during the late Miocene in Europe.

Keywords: Neogene, Europe, Diet, Environment, Ungulate

Zusammenfassung

Ziel der vorliegenden Untersuchung ist es, die ökologischen Nischen von Ruminantiern und Equiden der Untervallesischen Fundstelle Atzelsdorf (Österreich) zu charakterisieren und damit auch die vorherrschenden Umweltbedingungen. Hierzu werden die Ernährungspräferenzen dieser Huftiere anhand von „Microwear“- und „Mesowear“- Analysen bewertet. *Dorcatherium nauti* und *Micromeryx flourensianus* waren Blattäser, die auch Früchte fraßen, wohingegen der nachgewiesene Bovide (entweder *Miotragocerus* oder *Tethytragus*) ein Blattäser war. Auch die beiden Pferde *Hippotherium* sp. und *Anchitherium aurelianense* waren Blattäser. Die Abwesenheit von etwaigen Grasfressern in Atzelsdorf spricht eindeutig für eine Dominanz von Waldlandschaften um den Pannonsee zur Zeit des Vallesiums. Außerdem sprechen diese Ergebnisse für die ökologische Flexibilität von hochkronigen Hipparionen im späten Miozän Europas.

Schlüsselwörter: Neogene, Europa, Ernährung, Umwelt, Huftiere

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Introduction

The Atzelsdorf site, an abandoned gravel pit NW of Atzelsdorf village, is located about 35 km NE of Vienna in Lower Austria. It is situated at the western margin of the Vienna Basin. The deposits of the Atzelsdorf site belong to the Hollabrunn-Mistelbach Formation, which was discharged by the palaeo-Danube into Lake Pannon during the Late Miocene. Biostratigraphic investigations and well-logging correlations led to a correspondence of the Atzelsdorf fauna with the Vienna Basin Pannonian Zone C and an absolute age estimate of about 11.2-11.1 Ma (HARZHAUSER 2009, this volume), which corresponds to the early Vallesian mammal age. The Atzelsdorf locality is exceptional because of the co-occurrence of two genera of equids, the hipparionine *Hippotherium* (WOODBURNE 2009, this volume) and the anchiteriine *Anchiterium* (DAXNER-HÖCK & BERNOR 2009, this volume). This co-occurrence is rare in the fossil record because hipparionines dispersed in Europe from the early Vallesian mammalian age, while *Anchiterium* became extinct (ALBERDI et al. 2004).

The present study characterizes the ecological niche of this early hipparionine and more generally the niche partitioning amongst equids and ruminants. This allows the environmental conditions near the Atzelsdorf locality to be estimated. One focus is on examining how the new migrant and high-crowned hipparionines such as *Hippotherium* competed for food resources with ruminants. These were taxonomically diversified in Central Europe by then (Bovidae, Cervidae, Tragulidae, and Moschidae) (see HILLENBRAND et al. this volume). Unfortunately, specific inferences on niche partitioning between the two equids cannot be expected: the dental material of *Anchiterium* is poor.

The ecological relationships between equids and ruminants are investigated here based on feeding preferences. Many complementary approaches are available to estimate the diets of extinct species. Here, we combine two taxon-independent approaches, dental meso-wear and micro-wear analyses. The wear patterns on the cheek-teeth of herbivorous mammals are strongly linked to the physical properties of food items. While dental meso-wear patterns provide long-term information referred to as the “life-time” dietary signal, the dental micro-wear signature provides information about the properties of the food items consumed within a period of time shortly before death (TEAFORD & OYEN 1989).

Ungulates, whose main food resources are graminoids (including grasses, sedges, and rushes), bear many scratches on their dental shearing facets. This dense scratching in grazing ungulates is due to the high concentration of silica phytoliths in the cell walls of these monocotyledons (KAUFMAN et al. 1985). Conversely, a recent exploratory study (SANSON et al. 2007) concludes that micro-wear design might not be related to the abrasiveness of silica phytoliths but to the exogenous grit and dust deposited on food. This assumption, however, is contradicted by a careful examination of published micro-wear data on ungulates (grazers or browsers inhabiting either dry open landscapes or humid forested habitats). Instead, food items are apparently the main factors controlling the micro-wear genesis (see MERCERON et al. 2007a: 333-334). In contrast to monocotyledons, dicotyledons have fewer silica phytoliths. Consequently, browsing ungulates tend to have a higher ratio of pits to scratches compared to grazers. Beyond the grazer/browser dichotomy, the dental micro-wear design has been used to detect more subtle feeding preferences. For instance, browsers whose diets contain large amounts of both fruits

and seeds tend to have more scratches than the exclusive leaf eaters (MERCERON et al. 2007a; SOLOUNIAS & SEMPREBON 2002). Moreover, intermediate feeders have a wider spectrum of micro-wear patterns, pointing to flexible feeding preferences (MERCERON et al. 2007a, 2007b; SOLOUNIAS & MOELLEKEN 1992; SOLOUNIAS & SEMPREBON 2002).

Based on meso-wear pattern, grazing ungulates tend to have higher frequency of low occlusal molar reliefs with round or blunt cusps; occlusal relief and cusp shapes are the two relevant variables used to characterize dental meso-wear patterns. Browsers, on the other extreme, tend to have high occlusal reliefs with sharp or round cusps. However, browsers depending heavily in frugivory tend to have a more worn dental pattern than exclusive leaf browsers.

Material and methods

The dental micro-wear pattern can be investigated on both upper and lower cheek teeth, whereas the dental meso-wear analysis here is restricted to the upper dentition (tabs 1, 2; Appendix 1).

The fossil material belongs to unit 2 of the Atzelsdorf section, which represents the typical deposits of the Hollabrunn-Mistelbach Formation. A seventh unit covering the 6 underlying ones witnesses a transgression of Lake Pannon, an event dated at ca. 11.0-11.1 Ma (HARZHAUSER 2009, this volume). Ungulates are represented by *Hippotherium* sp., *Anchiterium aurelianense* (Equidae, Perissodactyla; WOODBURN this volume; BERNOR & DAXNER-HÖCK this volume), *Micromeryx flourensianus* (Moschidae, Artiodactyla), *Dorcatherium nauti* (Tragulidae, Artiodactyla), a bovid assigned either to *Miotragocerus* sp. or to *Tethytragus* sp. (Bovidae, Artiodactyla), and *Euprox* sp. (Cervidae, Artiodactyla; HILLENBRAND et al. this volume). This latter species is not included because of the lack of available dental material. The fossil material belongs to private collectors

Tab. 1. Summary statistics (mean m and standard deviation sd) on dental micro-wear variables (number of scratches N_s , number of pits N_p , and percentage of pits P_p) for extant and extinct species.

		N_s			N_p		P_p	
		N	m	sd	m	sd	m	sd
Extant grazers	<i>Equus burchellii</i>	24	22.7	4.7	12.0	8.0	32.1%	12.5%
	<i>Equus przewalskii</i>	6	29.8	3.7	11.7	5.1	27.2%	6.6%
	<i>Hippotragus niger</i>	13	27.7	3.9	14.2	7.2	32.3%	10.5%
Extant browsers	<i>Litocranius walleri</i>	16	15.1	2.3	34.5	19.5	66.6%	9.5%
	<i>Odocoileus virginianus</i>	11	19.9	5.8	31.1	10.8	60.1%	13.3%
	<i>Cephalophus dorsalis</i>	19	27.2	9.3	45.6	17.4	61.6%	14.3%
	<i>Hippotherium</i> sp.	8	13.9	4.0	56.9	16.0	79.6%	7.3%
Fossil species	<i>Dorcatherium nauti</i>	22	22.2	6.9	40.2	15.3	62.1%	16.4%
	<i>Anchiterium aurelianense</i>	1	18.0		75.0		80.6%	
	<i>Micromeryx flourensianus</i>	5	21.6	6.7	41.8	5.3	66.1%	9.6%
	Bovid	9	14.4	4.8	50.3	11.0	77.5%	6.4%

(indicated by S for collection SCHEBECZEK, Pellendorf or P for collection PENZ, Vienna followed by an identification number). public collections. The large majority of the specimens, however, are available as casts at the Naturhistorisches Museum of Vienna, Austria (NHMW) (Appendix 1).

The protocol of MERCERON et al. (2004, 2005) was applied for the micro-wear analysis. Because the fossil samples are small and heterogeneous in terms of tooth position, the dental micro-wear analysis was restricted to three main variables. These are depicted as significant to discriminate feeding preferences (MERCERON & MADELAINE 2006; MERCERON et al. 2007a; RIVALS & SOLOUNIAS 2007; SOLOUNIAS et al. 1988; SOLOUNIAS & SEMPREBON 2002). After scoring pits (Np) and scratches (Ns), the percentage of pits ($Pp = Np/Tot$) was computed (tab. 1). The dental micro-wear pattern of fossil species with unknown feeding habits was compared with those of six present-day species of ungulates with known differences in diet. *Hippotragus niger*, *Equus burchelli* and *E. przewalskii* represent the grazing species, whereas *Litocranius walleri*, *Odocoileus virginianus* and *Cephalophus dorsalis* compose the browsing cluster. The two latter browse on fruits and foliages, whereas *Litocranius walleri* is an exclusive leaf browser (GAGNON & CHEW 2000; GRUBB 1981; HALLS 1978; KING 2002; PERELADOVA et al. 1999; RAMIREZ et al. 1997; STEWART & STEWART 1970). The samples of these present-day species belong to a more extensive comparative database for dental micro-wear analysis (MERCERON et al. 2004, 2006, 2007a, 2007b). Comparisons between extant and extinct species were investigated through a single classification analysis of variance (tab. 3). Tukey's Honestly Significant Difference (HSD) and Fisher's Least Significant Difference (LSD) multiple comparisons tests were used to determine sources of significant variation. Results for pairwise tests are presented to balance risks of Type I and Type II errors given the large number of comparisons (tab. 4) (SOKAL & ROHLF 1998). In order to mitigate the violation of parametric test assumptions, all variables were first rank-transformed (CONOVER & IMAN 1981).

The protocol of FORTELIUS & SOLOUNIAS (2000) was applied for the dental meso-wear analysis. The data on fossil species (tab. 2) were then compared with the comparative database for dental meso-wear analyses published by FORTELIUS & SOLOUNIAS (2000). Cheekteeth were examined by the naked eye or using a low-magnification (12x) hand lens. Occlusal relief was classified as high (H) or low (L) according to the meso-wear convention of FORTELIUS & SOLOUNIAS (2000), which relates to the depth of the valley between the cusps. The second variable, cusp shape, included three scored attributes: sharp (S), round (R), and blunt (B) depending on the degree of facet development. A sharp cusp terminates at a point and has no rounded area between the mesial and distal

Tab. 2. Scoring of dental meso-wear pattern on upper dentition for fossil species. H: High occlusal relief; S, R, and B: Sharp, Round, and Blunt cusp shapes.

	N	HS	HR	HB	LS	LR	LB
<i>Dorcatherium nauii</i>	8	1	7	0	0	0	0
<i>Micromeryx flourensianus</i>	4	0	4	0	0	0	0
Bovid	5	2	3	0	0	0	0
<i>Hippotherium</i> sp.	5	0	0	0	0	5	0

facets. A rounded cusp has a distally smoothed tip, while a blunt cusp lacks distinct facets. These parameters were widely discussed and defined in previous studies (e.g., FORTELIUS & SOLOUNIAS 2000; KAISER 2003). Six conditions were thus identified: low relief with sharp [L-S], round [L-R] or blunt cusps [L-B] and high relief with sharp [H-S], round [H-R] or blunt cusps [H-B] (tab. 2). This latter category was uncommon. FORTELIUS & SOLOUNIAS (2000) scored such conditions for few individuals amongst grazing ungulates. No fossil specimen investigated here displayed such a dental meso-wear pattern.

Results and discussions

Despite the small sample sizes, the dental meso-wear patterns of the ruminants and *Hippotherium* clearly differ. The equid has a low occlusal relief with rounded cusps, whereas ruminants have a high occlusal relief with round and sharp cusps (tab. 2). The dental meso-wear pattern of *Hippotherium* points to a diet based on abrasive items (tab. 1; FORTELIUS & SOLOUNIAS 2000). Its dental micro-wear pattern, however, differs significantly from that of present-day grazing species. Rather, it displays similarities with browsing species (tabs 1, 2, 4, figs 1-2). This dental micro-wear pattern therefore excludes the sole consumption of graminoids for *Hippotherium* at Atzelsdorf. Furthermore, the very low-density scratches would indicate browsing habits similar to that of the extant *Litocranius walleri* (tabs 1, 2, 4, figs 1-2; MERCERON et al. 2007a, 2007b). The so intensive occlusal meso-wear pattern for *Hippotherium* associated with leaf-browsing habits, as depicted by the dental micro-wear analysis, might be due either to the ingestion of tough but not abrasive foods or to a high amount of foliage to counter-balance low nutrient values.

The dental micro-wear pattern of the only specimen of *Anchitherium* indicates that this individual had browsed a few days before dying (tab. 1, fig. 2). Such browsing habits

Tab. 3. Results of the ANOVAs with ranked data. Ns: number of scratches; Np: number of pits, and Pp: percentage of pits.

	<i>df</i>	SS	MS	F	<i>p</i>
Ns					
Effect	10	95283.9	9528.4	11.175	<0.001
Error	123	104877.6	852.7		
Total	133	200161.5			
Np					
Effect	10	129459.1	12945.9	22.449	<0.001
Error	123	70932.4	576.7		
Total	133	200391.5			
Pp					
Effect	10	130573.2	13057.3	22.970	<0.001
Error	123	69918.8	568.4		
Total	133	200492.0			

are consistent with the dental meso-wear design of the large-sized sample of *Anchitherium* from the Early/Middle Miocene of Sandelzhausen in southern Germany (KAISER in press).

The dental micro-wear patterns of the ruminants do not contradict the dental meso-wear results because all the tree ruminants have browsing micro-wear signatures. In fact, these three species have a higher percentage and number of pits than do grazers (tabs 1, 4, figs 1, 2). As noted in the introduction, a trend can be depicted amongst browsing species from the frequency of scratches on shearing facets. Amongst extant species, leaf browsers such as *L. walleri* tend to have fewer scratches than frugivore browsers such as *O. virginianus* and *C. dorsalis* (MERCERON et al. 2007a; SOLOUNIAS & SEMPREBON 2002). Amongst fossil ruminants, *Dorcatherium* has significantly more scratches than the bovid (tabs 1, 4; figs 1, 2). This points to differences in feeding habits. The tragulid was probably a frugivore, whereas the bovid specialized in leaf browsing. Although the sample size is low, a similar divergence of feeding habits is evident between the bovid and *Micromeryx* (tabs 1, 4, figs 1, 2). Indeed, MERCERON et al. (2007a) already demonstrated such a niche partitioning between the bovid *Miotragocerus* sp. and the moschid *Micromeryx flourensianus* in Rudabánya (Vallesian of Hungary). Based on both dental micro- and meso-wear analyses, the former is depicted as a leaf browser and *M. flourensianus* as a browser on fruits and seeds.

Conclusions

The total absence of grazing ungulates in the guild of meso-herbivorous mammals (mammals weighing from 4 to 450 kg) (FRITZ et al. 2002) clearly excludes the presence of a continuous herbaceous vegetal layer and consequently open landscapes at Atzels-

Tab. 4. Results on pairwise comparisons of extinct and extant species. Significance at $\alpha < 0.05$ is indicated in normal font for Fisher's LSD tests and in bold font for both Tukey's HSD and Fisher's LSD tests. Ns: number of scratches; Np: number of pits, and Pp: percentage of pits.

	Grazers			Browsers			Fossils		
	E. burchellii	E. przewalskii	H. niger	L. walleri	C. dorsalis	O. virginianus	Bovid	Hippotherium	Dorcatherium
Bovid	Pp Np Ns	Pp Np Ns	Pp Np Ns	Np Pp	Pp Ns	Pp Np Ns			
<i>Hippotherium</i>	Pp Np Ns	Pp Np Ns	Pp Np Ns	Np Pp	Pp Ns Np	Pp Np Ns			
<i>Dorcatherium</i>	Pp Np	Pp Np Ns	Pp Np Ns	Ns	Ns	Np	Pp Ns Np	Pp Ns Np	
<i>Micromeryx</i>	Pp Np	Pp Np	Pp Np				Ns	Pp Ns	

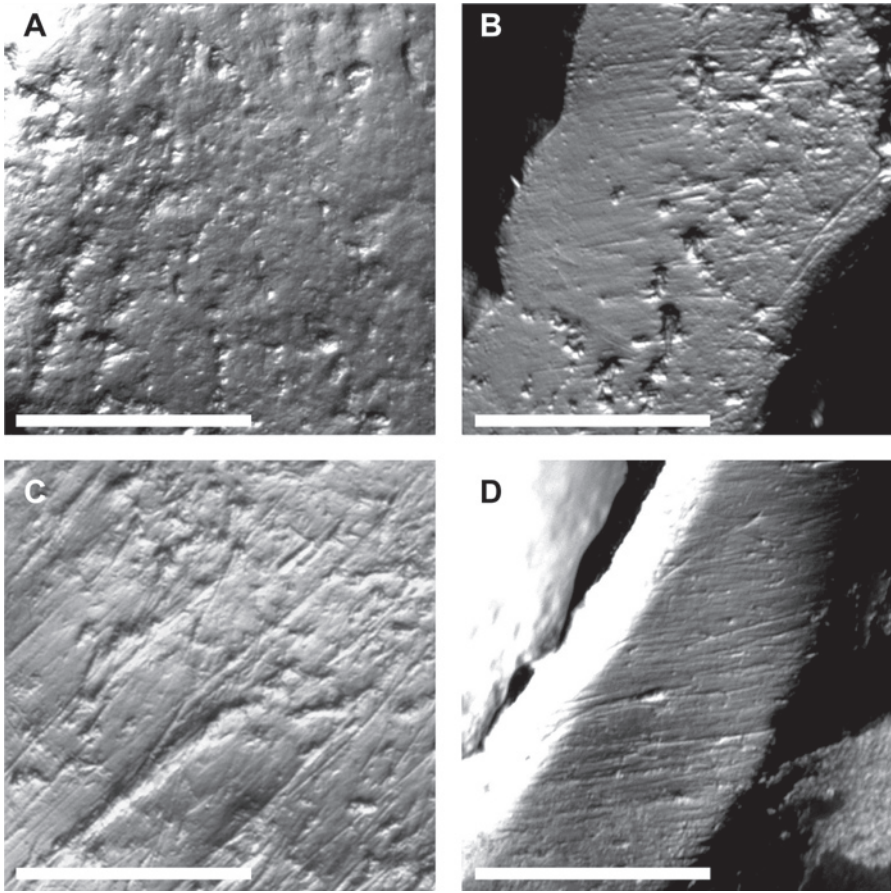


Fig. 1. Light micrographs showing the dental micro-wear pattern on the molar shearing facets of *Hippotherium* sp. (A; NHMW 2008z0062/0008-S142), the undetermined bovid (B; NHMW 2008z0051/0009-S128), *Dorcatherium navi* (C; NHMW 2008z 0049/0003-S15), and *Micromeryx flourensianus* (NHMW 2008 z 0050/0001-S35). Scale bar = 500 μ m.

dorf during the early Vallesian. *Hippotherium* and the bovid (either *Miotragocerus* or *Tethyragus*), being leaf-browsers, along with the presence of two browsing ruminants (*Micromeryx* and *Dorcatherium*) that fed at least partly as frugivores, indicate forested habitats around Atzelsdorf during the Early Vallesian. These conclusions are consistent with previous studies demonstrating forested landscapes in the Central European province during Vallesian times (BONIS et al. 1992; ERONEN & RÖSSNER 2007; FORTELIUS et al. 2003; MERCERON et al. 2007a).

Our results support forested habitats for the equids and the ruminants. A large spectrum of feeding preferences has been already pointed out for other Old and New World populations of hipparionines (HAYEK et al. 1992; KAISER 2003; KAISER et al. 2003; KOUFOS et al. 2006; MAC FADDEN et al. 1999; MERCERON et al. 2007a). Nonetheless, browsing and mixed dietary habits of early populations of hypsodont equids in Western and Central

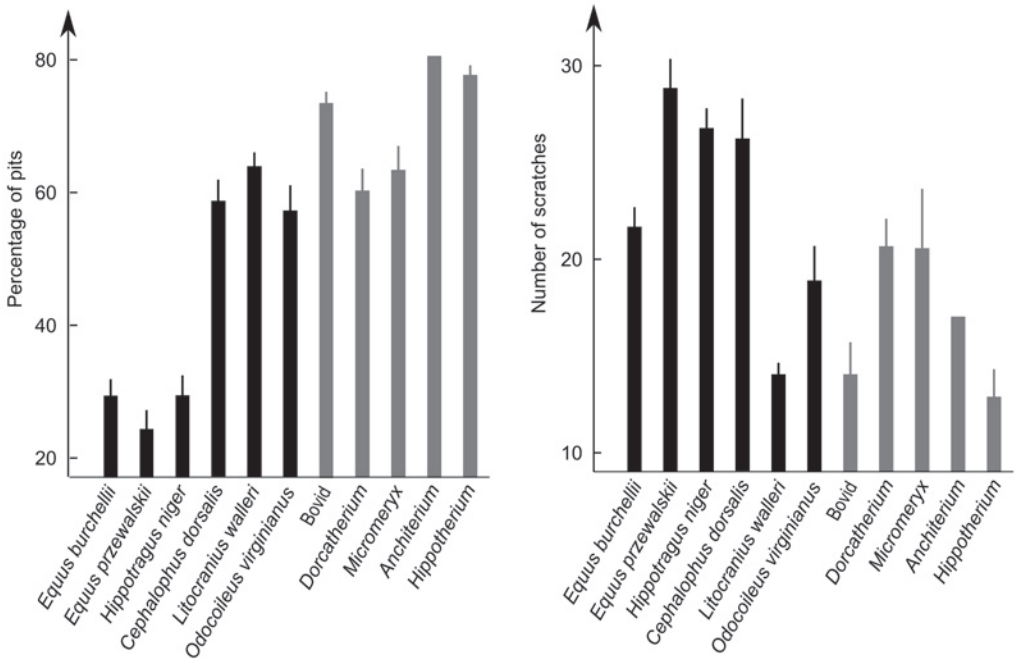


Fig. 2. Mean and standard error of the mean values for the variable Ns (number of scratches) and Pp (percentage of pits) for extant ungulates (black) and extinct species from Atzeldorf (gray).

Europe gave rise to many questions. Did earliest Eurasian hipparionines exploit open areas or did they compete with ruminants for access to browsing? In other words, was hypsodonty a constraint to exploit solely the open and grassy areas, or a selective advantage to widen their ecological niches after their dispersion through Eurasia? Our results, combined with those of previous studies, tend to support the latter hypothesis. Further multi-approach analyses on larger samples will undoubtedly increase our knowledge on the selective advantage of hypsodonty for access to food resources.

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References

- ALBERDI, M.T., GINSBURG, L. & RODRIGUEZ, J. (2004): *Anchitherium aurelianense* (Mammalia, Equidae) (Cuvier, 1825) dans l'Orléanien (Miocène) de France. – *Geodiversitas*, **26**: 115-155.

- BONIS, L. DE, BOUVRAIN, G., GERAADS, D. & KOUFOS, G.D. (1992): Multivariate study of the late Cenozoic mammalian faunal compositions and paleoecology. – *Paleontologia i Evolucio*, **24-25**: 93-101.
- CONOVER, W.J. & IMAN, R.L. (1981): Rank transformations as a bridge between parametric and nonparametric statistics. – *American Statistician*, **35**: 124-1129.
- DAXNER-HÖCK, G. & BERNOR, R.L. (2009): The Early Vallesian vertebrates from Atzelsdorf (Austria, Late Miocene). 8. *Anchitherium*, Suidae and Castoridae (Mammalia). – *Annalen des Naturhistorischen Museum Wien, Serie A*, **111**: 557-584
- ERONEN, J. & RÖSSNER, G.E. (2007): Wetland paradise lost: Miocene community dynamics in large herbivorous mammals from the German Molasse Basin. – *Evolutionary Ecology Research*, **9**: 471-494.
- FORTELIUS, M. & SOLOUNIAS, N. (2000): Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. – *American Museum Novitates*, **3301**: 1-36.
- , ERONEN, J., LIU, L., PUSHKINA, D., TESAKOV, A., VISLOBOKOVA, I. & ZHANG, Z. (2003): Continental-scale hypsodonty patterns, climatic paleobiogeography and dispersal of Eurasian Neogene large mammal herbivores. – In: REUMER, J.W.F. & WESSELS, W. (eds): *Distribution and migration of tertiary mammals in Eurasia*. – pp. 1-11, (DEINSEA).
- FRITZ, H., DUNCAN, P., GORDON, I.J. & ILLIUS, A.W. (2002): Megaherbivores influence trophic guilds structure in African ungulate communities. – *Oecologia*, **131**: 620-625.
- GAGNON, M. & CHEW, A.E. (2000): Dietary preferences in extant African Bovidae. – *Journal of Mammalogy*, **8**: 490-511.
- GRUBB, P. (1981): *Equus burchelli*. – *Mammalian species*, **157**: 1-9.
- HALLS, K.L. (1978): White-tailed deer. – In: SCHMIDT, J.L. & GILBERT, D.L. (eds): *Big Game of North America*. – pp. 43-65, Harrisburg PA (Stackpole Books).
- HAYEK, C.L.-A., BERNOR, R.L., SOLOUNIAS, N. & STEIGERWALD, P. (1992): Preliminary studies of Hipparionine horse diet as measured by tooth microwear. – *Annales Zoologici Fennici*, **28**: 187-200.
- HARZHAUSER, M. (2009). The Early Vallesian vertebrates from Atzelsdorf (Austria, Late Miocene). 2. Geology. – *Annalen des Naturhistorischen Museum Wien, Serie A*, **111**: 479-488
- HILLENBRAND, V, GÖHLICH, U.B. & RÖSSNER, G.E. (2009): The Early Vallesian vertebrates from Atzelsdorf (Austria, Late Miocene). 7. Ruminantia. – *Annalen des Naturhistorischen Museum Wien, Serie A*, **111**: 519-556
- KAISER, T.M. (in press): *Anchitherium aurelianense* (Equidae, Mammalia) – a brachyodont “dirty browser” in the community of herbivorous large mammals from Sandelzhausen (Miocene, Germany). – *Paläontologische Zeitschrift*
- (2003): The dietary regimes of two contemporaneous populations of *Hippotherium primigenium* (Perissodactyla, Equidae) from the Vallesian (Upper Miocene) of Southern Germany. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **198**: 381-402.
- , BERNOR, R.L., SCOTT, R.S., LORENZ FRANZEN, J. & SOLOUNIAS, N. (2003): New Interpretations of the Systematics and Palaeoecology of the Dorn-Dürkheim 1 Hipparions (Late Miocene, Turolian Age [MN11]), Rheinhessen, Germany. – *Senckenbergiana lethaea*, **83**: 103-133.

- KAUFMAN, P.B., DAYANANDAN, P. & FRANKLIN, C.I. (1985): Structure and function of silica bodies in the epidermal system of grass bodies. – *Annals of botany*, **55**: 487-507.
- KING, S.R.B. (2002): Home range and habitat use of free ranging Przewalski horses at Hustai National Park, Mongolia. – *Applied Animal Behaviour Science*, **78**: 103-113.
- KOUFOS, G.D., MERCERON, G., KOSTOPOULOS, D.S., VLACHOU, T.D. & SYLVESTROU, I.A. (2006): The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 11. Palaeoecology and Palaeobiogeography. – *Palaeontographica A*, **276**: 201-221.
- MAC FADDEN, B.J., SOLOUNIAS, N. & CERLING, T.E. (1999): Ancient Diets, Ecology, and Extinction of 5-Million-Year-Old Horses from Florida. – *Science*, **283**: 824-827.
- MERCERON, G. & MADELAINE, S. (2006): Molar microwear pattern and palaeoecology of ungulates from La Berbie (Dordogne, France): environment of Neanderthals and modern human populations of the Middle/Upper Palaeolithic. – *Boreas*, **35**: 272-278.
- , VIRIOT, L. & BLONDEL, C. (2004): Tooth microwear pattern in roe deer (*Capreolus capreolus*, L.) from Chizé (Western France) and relation to food composition. – *Small Ruminant Research*, **53**: 125-138.
- , SCHULTZ, E., KORDOS, L. & KAISER, T.M. (2007a): Palaeoenvironment of *Dryopithecus brancoi* at Rudabánya, Hungary: evidence from dental meso- and micro-wear analyses of large vegetarian mammals. – *Journal of Human Evolution*, **53**: 331-349.
- , BLONDEL, C., BONIS, L. DE, KOUFOS, G.D. & VIRIOT, L. (2005): A new dental microwear analysis: application to extant Primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). – *Palaios*, **20**: 551-561.
- , ZAZZO, A., SPASSOV, N., GERAADS, D. & KOVACHEV, D. (2006): Bovid paleoecology and palaeoenvironments from the late Miocene of Bulgaria: evidence from dental microwear and stable isotopes. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **241**: 637-654.
- , BLONDEL, C., VIRIOT, L., KOUFOS, G.D. & BONIS, L. DE (2007b): Dental microwear analysis on bovids from the Vallesian (Late Miocene) of the Axios Valley in Greece: reconstruction of the habitat of *Ouranopithecus macedoniensis* (Primates, Hominoidea). – *Geodiversitas*, **29**: 421-433.
- , BLONDEL, C., BRUNET, M., SEN, S., SOLOUNIAS, N., VIRIOT, L. & HEINTZ, E. (2004): The late Miocene palaeoenvironment of Afghanistan as inferred from dental microwear in artiodactyls. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **207**: 143-163.
- PERELADOVA, O.B., SEMPÉRÉ, A.J., SOLDATOVA, N.V., DUTOV, V.U., FISENKO, G. & FLINT, V.E. (1999): Przewalski's horse-adaptation to semi wild life in desert conditions. – *Oryx*, **33**: 47-58.
- RAMIREZ, R.G., QUINTANILLA, J.B. & ARANDA, J. (1997): White-tailed deer food habits in northeastern Mexico. – *Small Ruminant Research*, **25**: 141-146.
- RIVALS, F. & SOLOUNIAS, N. (2007): Differences in tooth microwear of population of Caribou (*Rangifer tarandus*, Ruminantia, Mammalia) and implications to ecology, migration, glaciations and dental evolution. – *Journal of Mammalian Evolution*, **14**: 182-192.
- SANSON, G.D., KERR, S.A. & GROSS, K.A. (2007): Do silica phytoliths really wear mammalian teeth? – *Journal of Archaeological Science*, **34**: 526-531.
- SOKAL, R.R. & ROHLF, J.F. (1998): *Biometry: The principles and practice of statistics in biological research*. – 887 pp., New York (Freeman & Co).

- SOLOUNIAS, N. & MOELLEKEN, S.M.C. (1992): Dietary adaptation of two goat ancestors and evolutionary considerations. – *Geobios*, **25**: 797-809.
- & SEMPREBON, G. (2002): Advances in the reconstruction of ungulates ecomorphology with application to early fossil equids. – *American Museum Novitates*, **3366**: 1-49.
- , TEAFORD, M.F. & WALKER, A. (1988): Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. – *Paleobiology*, **14**: 287-300.
- STEWART, D.R.M. & STEWART, J.S. (1970): Comparative food preferences of five East African ungulates at different seasons. – In: DUFFEY, E. & WATT, A.S. (eds): *The Scientific Management of Animal and Plant Communities for Conservation*. – pp. 351-366, Oxford (Blackwell Scientific Publications).
- TEAFORD, M.F. & OYEN, O.J. (1989): *In vivo* and *in vitro* turnover in dental microwear. – *American Journal of Physical Anthropology*, **80**: 447-460.
- WOODBURNE, M.O. (2009): The Early Vallesian vertebrates from Atzelsdorf (Austria, Late Miocene). 9. *Hippotherium* (Mammalia, Equidae). – *Annalen des Naturhistorischen Museum Wien, Serie A*, **111**: 585-604

Appendix 1. List of fossil material including specimen number, taxonomic assignment, tooth position, and mesowear scoring and microwear counting per area (300 x 300µm).

Anchiterium aurelianense

Specimen	Tooth position	Mesowear	Ns	Np	Pp
P22	UM12		18	75	80.6

Dorcatherium naui

Specimen	Tooth position	Mesowear	Ns	Np	Pp
NHMW 2008z0049/0026 – P15	m3 dex		28	49	63.6
PNN	M1/2/3	HS	7	48	87.3
NHMW 2008z0049/0029 – S115	m1 dex		20.5	36	63.4
NHMW 2008z0049/0008 – S116	m2 dex		30	49	62.0
NHMW 2008z0049/0009 – S117	m1 sin		22	39	63.9
NHMW 2008z0049/0011 – S120	M1 dex	HR	13	51	79.7
S121	M1/2/3 sin		10	63	86.3
NHMW 2008z 0051/0013 – S133	M3 dex	HR			
NHMW 2008z0049/0015 – S134	m1 sin		29	19	39.6
NHMW 2008z0049/0023 – S138	M2 sin		25	38	60.3
NHMW 2008z0049/0003 – S15	m3 dex		26	53	67.1
NHMW 2008z0049/0004 – S16	m3 sin		25	55	68.8
NHMW 2008z0049/0005 – S17	M1/2/3 dex	HR	12	55	82.1
S20	M1/2/3	HR			
NHMW 2008z0049/0030 – S30	m1/2 dex		23	6	20.7
NHMW 2008z0049/0021 – S31	m2 dex		33	42	56.0
NHMW 2008z0049/0040 – S33	m1 dex		21	51	70.8
NHMW 2008z0049/0001 – S6	M2 dex	HR	30	38	55.9
S63	UM12	HR	25	28	52.8
NHMW 2008z0049/0016 – S64	D4 dex		23	59	72.0
NHMW 2008z0049/0028 – S67	m1 sin		23	15	39.5
NHMW 2008z0049/0019 – S86	m3 dex		15	38	71.7
NHMW 2008z0049/0002 – S9	M2 sin	HR	22	35	61.4
NHMW 2008z0049/0031 – S97	m2 dex		26	18	40.9
NHMW 2008z0049/0029	m1 dex		22	31	58.5

Hippotherium sp.

Specimen	Tooth position	Mesowear	Ns	Np	Pp
NHMW 2008z0062/0000 – S102	pm/m fragment		8	57	87.7
NHMW 2008z0062/0003 – S103	M1 dex	LR	12	67	84.8
NHMW 2008z0062/0005 – S106	P2 dex		13	49	79.0
NHMW 2008z0062/0006 – S107	P4 dex	LR	19	50	72.5
NHMW2008z0062/0011 – S110	M1 dex	LR			
S111	M1 dex	LR	17	43	71.7
NHMW 2008z0062/0008 – S142	m3 dex		11	92	89.3
NHMW 2008z0062/0001 – S22	P3 dex		12	50	80.6
NHMW 2008z0062/0002 – S24	M2 dex	LR	19	47	71.2

Micromeryx flourensianus

Specimen	Tooth position	Mesowear	Ns	Np	Pp
NHMW 2008z0050/0007 – P10	M1/2/3? sin	HR			
NHMW 2008z0050/0008 – P11	m3 sin		19	44	69.8
NHMW 2008z0050/0006 – P9	m2 sin		22	42	65.6
NHMW 2008z0050/0001 – S35	m2 dex		33	33	50.0
NHMW 2008z0050/0002 – S54	M1/2/3? sin	HR			
NHMW 2008z0050/0004 – S56	D4 dex		18	43	70.5
S60	m1/2? sin				
S61	M1/2/3? sin	HR	16	47	74.6
NHMW 2008z0050/0010	M1/2/3? sin	HR			

Bovid

Specimen	Tooth position	Mesowear	Ns	Np	Pp
NHMW 2008z0051/0015 – P18	M2 sin		12	44	78.6
S100	m12 sin		13	54	80.6
NHMW 2008z0051/0001 – S11	M2 sin	HS	15	49	76.6
NHMW 2008z0051/0002 – S12	M2 dex	HR			
NHMW 2008z0051/0009 – S128	m2 sin		20	53	72.6
NHMW 2008z0051/0003 – S13	M1 sin	HS			
NHMW 2008z0051/0012 – S131	M1 dex	HR	24	45	65.2
NHMW 2008z0051/0014 – S136	M3 dex	HR	9	39	81.3
S14	m2 sin		14	57	80.3
NHMW 2008z0051/0004 – S18	m2 dex		13	38	74.5
S124	M12 dex		10	74	88.1

