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Straight from the horse's mouth: High-resolution proxies for the study of horse diet and its relation to the seasonal occupation patterns at Divnogor'ye 9 (Middle Don, Central Russia)

Florent Rivals^{a, b, c, *}, Keiko Kitagawa^{d, e}, Marie-Anne Julien^d, Marylène Patou-Mathis^d, Alexander A. Bessudnov^f, Alexander N. Bessudnov^g

^a ICREA, Pg. Lluís Companys 23, 08010, Barcelona, Spain

^b Institut Català de Paleocologia Humana i Evolució Social (IPHES), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007, Tarragona, Spain

^c Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002, Tarragona, Spain

^d Unité Histoire Naturelle de l'Homme Préhistorique (UMR 7194), CNRS, MNHN, UPVD, 1 rue René Panhard, 75013, Paris, France

^e Department of Early Prehistory and Quaternary Ecology, University of Tübingen, Schloss Hohentübingen, Tübingen, 72070, Germany

^f Institute for the History of Material Culture, Russian Academy of Sciences, Dvortsovaya Nab. 18, 191186, Saint Petersburg, Russia

^g P.P. Semenov – Tyan-Shanskii Lipetsk State Pedagogical University, Lenina st. 42, 398020, Lipetsk, Russia

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ABSTRACT

In this study, we present the results of tooth mesowear and microwear analyses on fossil horses recovered in two Late Pleistocene archaeological layers at Divnogor'ye 9 (Middle Don, Central Russia). Tooth wear refers to two high-resolution proxies for reconstructing dietary habits in ungulates which give access to different periods in life history of the animals sampled. Mesowear is a proxy averaging diet over months, while microwear reflects the diet of the last days before death. The first objective of this study is to integrate and compare the results from mesowear and microwear to investigate the dietary habits of the studied fossil horses (*Equus ferus*), to reconstruct their habitat(s), and compare with stable isotope and indirect proxies. The second objective is to participate to disentangle the various hypotheses of site formation and the nature of accumulation of the horse remains.

The horse populations around Divnogor'ye 9 likely lived in habitats where both grass and browse were available, but our analysis indicates that they were selectively and exclusively feeding on grass. Furthermore, we used tooth microwear pattern as a high-resolution proxy for estimating the duration of mortality events and their seasonality. The application of a well standardized approach to interpret the microwear data permitted us to classify the two assemblages as seasonal events. The results support the hypothesis that the two accumulations of the horse remains represent seasonal, repeated occupations of the site by Late Glacial hunters in the same season for hunting and mass killing of horses. This study highlights the advantage of using non-destructive sampling methods in a multidisciplinary approach when investigating ungulate diets and patterns of fossil accumulations in archaeological sites.

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1. Introduction

The integrated use of high-resolution techniques on archaeological faunal material has increased in the recent years to reconstruct ancient human subsistence strategies (Rendu, 2007; Julien

et al., 2012, 2015; Sánchez-Hernández et al., 2014, 2016; Balasse et al., 2017; Tornero et al., in press). The recent advances in the application of these techniques to archaeological sites are providing relevant data about hominid behavior and ecology. Among those, the study of mortality events of large game at prehistoric sites is key for understanding seasonal resource procurement by hominins (e.g. Farizy et al., 1994; Speth, 1997, 2010; Fenner, 2009; Julien, 2007, 2009; Hoffecker et al., 2010; Carlson and Bement, 2013; Rendu et al., 2012; Lubinski, 2013; Julien et al., 2015; Rivals et al., 2015a; Rodríguez-Hidalgo et al., 2016).

In this study, we use an integrated approach, combining two

* Corresponding author. Institut Català de Paleocologia Humana i Evolució Social (IPHES), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007, Tarragona, Spain.

E-mail address: frivals@iphes.cat (F. Rivals).

methods of tooth wear analysis, mesowear and microwear and compare our results with other direct (stable isotope) and indirect proxies (pollen, faunal analyses, lithic remains, etc.). Tooth mesowear analyzes the shape of wear facet to evaluate the abrasiveness of the diet in ungulates. Mesowear is a (palaeo)ecological proxy which reflects the diet of the last weeks or months before the death of an animal and thus indicates dietary preferences on an ecological scale (Fortelius and Solounias, 2000). Tooth microwear patterns, microscopic features produced by food items on the teeth, reflect the diet of the last days of life of an animal (Grine, 1986; Solounias and Semprebon, 2002). Consequently, microwear is a high-resolution proxy for estimating the diet at the time of death, and can be used for assessing the duration of accumulation events in archaeological sites and their seasonality. This approach allows researchers to differentiate assemblages which accumulated in a seasonal or shorter event, events longer than a season, and separated events occurring in different seasons (Rivals et al., 2015a, 2015b). Therefore, the integration of dental wear offers new doors to investigating seasonal patterns of ungulate accumulations in archaeological sites using non-destructive sampling.

For this approach, we analyzed two sets of samples from two horse bone beds of the well-preserved Late Paleolithic site of Divnogor'ye 9 (Middle Don, Central Russia). Despite the more than ten-year history of the site research, there are several debated views regarding the formation of the bone accumulations and the nature of human activity at the site. According to Bessudnov and Bessudnov (2010) and Bessudnov et al. (2012, 2013), Divnogor'ye 9 is considered as a place for periodic mass killing and primary butchering of wild horses. On the other hand, Lavrushin et al. (2010, 2011) proposed that most of the bones' horizons are of natural origin in Divnogor'ye 9 and were formed due to repeated mudflows that caused the death of horses. Kuznetsova et al. (submitted)

suggested that the horses died of starvation at the end of winter or early spring, and that they died at the top of the ravine and then were redeposited by temporary flows to the entrance of the ravine.

In this context, this study has two objectives: (1) to investigate the diet of the horse at two temporal scales: ecological i.e. annual average (through mesowear), and at the time of death (through microwear), and (2) to inform about the duration and seasonality of accumulation(s) of the horse assemblages in layers 5 and 6 of Divnogor'ye 9 using the variability of the microwear signal to provide new evidence to explain the formation of the site.

2. Divnogor'ye 9

Divnogor'ye 9 (also spelled Divnogorie 9) is an open air archaeological site on the bank of the Tikhaya Sosna River, a tributary of the Don River, at the southern margin of the Central Russian Upland in the Voronezh Region (50° 57' N, 39° 18' E) (Fig. 1). More precisely, the site is located in a gully of a chalk plateau, without permanent water, which formed during the Last Glacial period. The 16 m deep excavation exposed the entire stratigraphic profile down to the valley bottom, which is characterized by lacustrine sediments in the lower part of the profile overlain by paleosols and slope deposits (Lavrushin et al., 2010, 2011; Bessudnov et al., 2013; Sycheva et al., 2016).

Divnogor'ye 9 is comprised of seven layers, all yielding faunal remains. The layers where the samples come from were accumulated during the Raunis interstadial (14.5–13.4 ka uncal BP). Likely deposited in a relatively short period, they have been dated of $14,430 \pm 160$ (AA-90655, Layer 6) and $13,900 \pm 140$ BP (AA-90654, Layer 5) (Lavrushin et al., 2011) (Fig. 2). The pollen record of the lacustrine sediment indicates that grasses and dwarf shrubs including *Artemisia* and *Chenopodiaceae* were common while pine

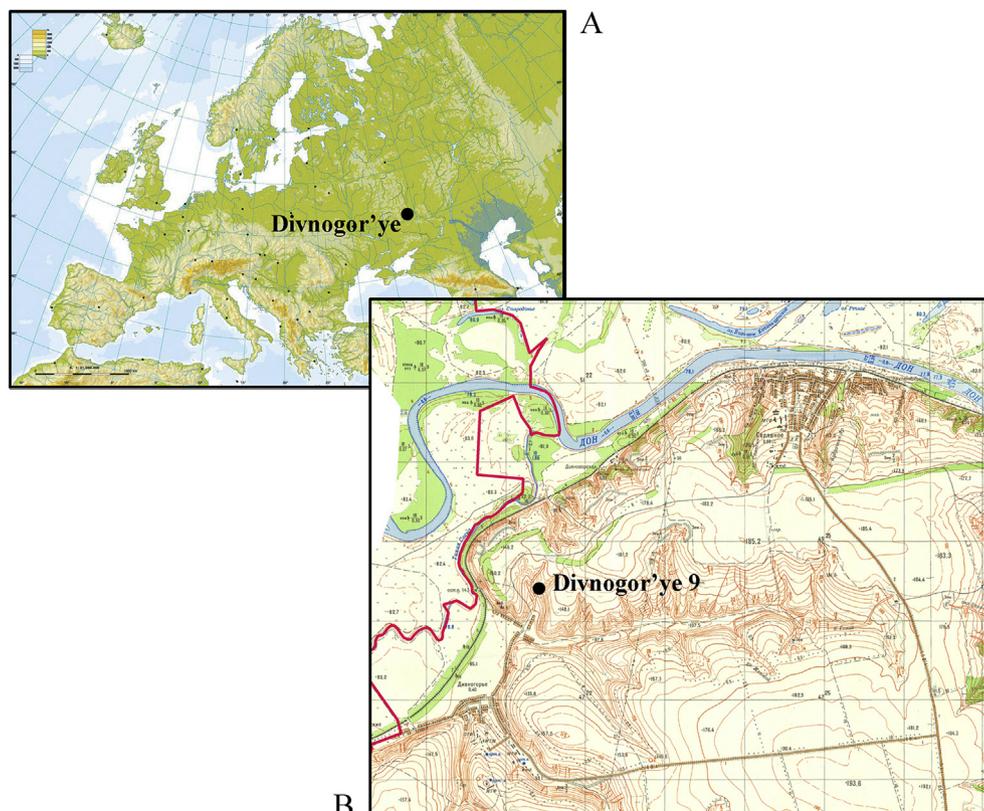


Fig. 1. A. General map of the location of Divnogor'ye 9. B. Topographic map of the location of the site.

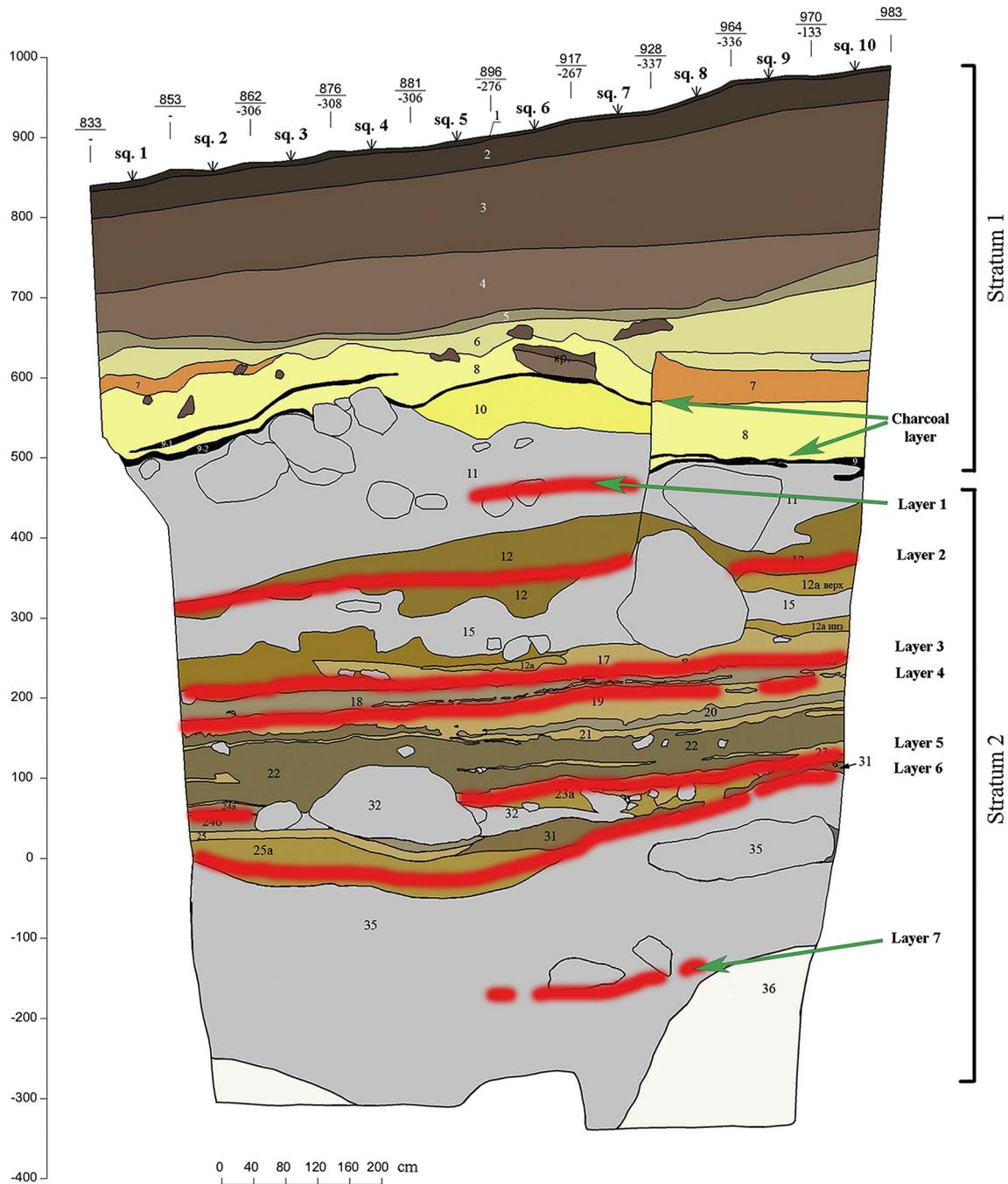


Fig. 2. Chrono-stratigraphy of Divnogor'ye 9. Excavation area 1, western section (2012). After Bessudnov et al. (2013).

was the dominant tree species (Arslanov et al., 1999; Lavrushin et al., 2010). The lithic assemblage composed roughly of 200 pieces from all cultural layers. It is characterized by truncated blades, double-truncated blades, backed bladelets, burins on truncations and endscrapers. Based on the lithic assemblages and the radiocarbon chronology, the site is attributed to the Late Epi-gravettian (Bessudnov and Bessudnov, 2016).

The faunal remains are more abundant. Wild horse (*Equus ferus*) is clearly the dominant species, with more than 99.9% of the faunal assemblages from all the stratigraphic layers. Three other species (polar fox, wolverine and hare) are represented by a single specimen (Bessudnov et al., 2012). The horse remains are particularly abundant in Layers 3, 5 and 6, both in terms of number of identified

specimens (NISP) and minimum number of individuals (MNI). In these layers, the skeletal representation is even and there is no evidence of natural attrition, suggesting no significant bias against the fragile elements (Kuznetsova et al., in press). Many bones were complete and/or in anatomical connection, and individuals were easily identifiable. In contrast, the remains of horses from layers 1, 2, and 4 consist of disarticulated, and isolated finds.

In all layers, the surfaces of the bone remains are relatively well-preserved with little to moderate weathering. No traces of carnivore damage have been observed. The evidence of butchery marks is relatively scarce, with cut marks occurring on ribs and costal cartilages.

For Layer 5 and 6, the age groups based on the tooth eruption

and wear indicate that the two archaeological populations consist predominantly of prime adults, with the presence of some calves and a small number of old adults. In addition, four specimens from layer 5 yielded seasonality data based on tooth eruption. Two indicated death during spring while the other two died between the end of fall to the beginning of winter. In level 6, only one specimen provided data about seasonality, one juvenile individual died in spring or summer (Kuznetsova et al., submitted).

Equid molars deriving from six sub-adult individuals from layer 5, previously sampled for dental-wear analysis, underwent stable isotopic analyses. The $\delta^{13}\text{C}$ values of Divnogor'ye 9 layer 5 horse's enamel carbonate ranges between -10.0‰ and -10.9‰ , with an average of -10.5‰ (Table 1). The values are consistent with other stable isotopic records from the steppe ungulates from the Late Pleistocene, both from Eastern and Western Europe (Julien, 2009; Julien et al., 2012; Yravedra et al., 2016). The $\delta^{13}\text{C}$ value of plants consumed by equids reflects an exclusive consumption of C_3 forage from an open steppic or grassland landscape, with no intake of C_4 plants, as expected for a Pleistocene Eurasian context (Tieszen, 1991). However, the horses sampled might have been feeding selectively, and one cannot exclude the possibility that other types of vegetation were available but not exploited by the specimens studied here, as suggested by the pollen record (cf. above, Lavrushin et al., 2010).

3. Material and methods

The material analyzed is currently stored at the Natural Architectural Archaeological Museum-Reserve "Divnogor'ye" (Liski Area of Voronezh Region). Dental specimens were studied through tooth mesowear and microwear analyses to assess dietary traits of horses in the assemblages from layers 5 and 6, the richest layers yielding NISP of 3583 and 2105, respectively (Kuznetsova et al., submitted). The two techniques provide dietary information on two different timescales: mesowear averages the diet over a few months or years (Fortelius and Solounias, 2000), while microwear reveals the diet in the last days of an animal's life (Grine, 1986). A total of 26 upper molars were selected and molded, i.e. 15 specimens from layer 5 and 11 from layer 6. The raw data have been published in Mendeley Data (Rivals, 2017) and are available at: <https://doi.org/10.17632/rd23dy9ksn.2>.

3.1. Tooth mesowear

Mesowear analysis is a method used to categorize 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 (Fortelius and Solounias (2000). Mesowear is scored macroscopically from the buccal side of upper molars, preferably the paracone of M2 (Fortelius and Solounias, 2000). A diet with low levels of abrasion

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 results in more rounded and blunted buccal cusp apices. Recent work based on empirical results showed that mesowear is more likely to reflect grazing in particular rather than the ingestion of soil or dust (e.g., Kaiser et al., 2013; Kubo and Yamada, 2014; Saarinen and Lister, 2016). 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) and therefore suitable for dietary reconstruction.

In this study, we used the standardized method (mesowear 'ruler') introduced by Muhlbachler et al. (2011). The method is based on seven cusp types (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). The average value of the mesowear data from a single sample corresponds to the mesowear score (MWS) (Muhlbachler et al., 2011).

3.2. Tooth microwear

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the cleansing, molding, casting, and examination protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). In short, the occlusal surface of each specimen was cleaned using acetone and then 96% alcohol. The surface was molded using high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. All specimens molded were carefully screened under the stereomicroscope. Those with badly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh features made during the collecting process or during storage) were removed from the analysis following King et al. (1999). Casts were observed under incident light with a Zeiss Stemi 2000C stereomicroscope at $35\times$ magnification, using the refractive properties of the transparent cast to reveal microfeatures on the enamel.

Microwear scars (i.e., elongated scratches and rounded pits) were quantified on the paracone of the upper teeth in a square area of 0.16 mm^2 using an ocular reticule. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004) as follows: pits (small and large pits, puncture pits), scratches (fine, coarse, hypercoarse), and gouges. Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, while

Table 1

Carbon isotope measurements (average, maximum and minimum) from enamel bioapatite of 6 individual horses from Divnogor'ye 9, layer 5.

Quadrant	Lab Nb.	Tooth	Total length of tooth (mm)	Nb. of samples	$\delta^{13}\text{C}$ mean	$\delta^{13}\text{C}$ max	$\delta^{13}\text{C}$ min
48	Di-3	Upper M3	72.7	19	-10.6	-8.4	-11.2
48	Di-4	Upper M3	68.9	13	-10.9	-10.6	-11.2
48	Di-5	Upper M1	66	19	-10.5	-9.6	-10.9
48	Di-6	Upper M3	75	14	-10.0	-9.0	-10.4
34	Di-8	Lower M3	80.9	16	-10.5	-10.3	-11.1
49	Di-10	Lower M2	65	11	-10.8	-10.2	-11.2
Average					-10.5		

The method of treatment is derived from Lee-Thorp and van der Merwe (1991) in Balasse et al. (2002) with the exception that the samples underwent two rounds of 0.1 M acetic acid treatment.

scratches are elongated microfeatures that are not merely longer than they are wide, but have straight, parallel sides. Large pits are deeper, generally at least about twice the diameter of small pits, and often have less regular outlines than do small pits. Gouges are features which have ragged, irregular edges and are much larger and deeper than large pits. Cross scratches are oriented somewhat perpendicularly to the majority of scratches observed on tooth enamel. In addition, scratch textures were assessed as being either fine, coarse, or a mixture per tooth surface. The scratch width score (SWS) is obtained 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 (Rivals et al., 2007b). Individual scores for a sample were then averaged to get the SWS.

The results were compared with a database constructed from extant ungulate taxa (Solounias and Semprebon, 2002). Using average scratch and pit data, it is possible to discriminate between the dietary categories of browser (i.e., eating woody and non-woody dicotyledonous plants) versus grazer (i.e., eating grass). Mixed feeding ungulates can best be separated from browsers or grazers by calculating the percentage of individuals in a population with scratch numbers that fall between 0 and 17 scratches in the 0.16 mm² area (%0–17) (Semprebon and Rivals, 2007). Thus, for extant ungulates, the percentages of individuals in the low-scratch range are generally as follows: grazers with 0.0–22.2%; mixed feeders with 20.9–70.0%; and leaf browsers with 72.7–100.0% (Semprebon and Rivals, 2007).

Finally, following Rivals et al. (2015b), two measurements of variability of scratch density, namely the standard deviation (SD) and the coefficient of variation (CV) are used to estimate the relative duration of the mortality event(s) of the horses from Divnogor'ye 9 layers 5 and 6. The SD and CV values are plotted on a heat map which space is divided in three areas, each one corresponding to a different type of accumulation event(s): [A] Season-long or shorter time windows, [B] event longer than a season, and [C] separated events that occurred in different non-contiguous seasons (Rivals et al., 2015b). The color scale on each side of the boundaries between each area represents the different probability of error.

4. Results

The preservation of the sampled material from Layer 5 and 6 of Div. 9, both for tooth mesowear and microwear, is excellent. All the specimens sampled were suitable for mesowear analysis, and 93% of the specimens from layer 5 and 100% from layer 6 were suitable for microwear analysis. This particularly good state of preservation supports the observations made in the field that horses were quickly buried after their death (Bessudnov et al., 2012, 2013).

4.1. Dietary traits at the time of death

The mesowear pattern on the horse molars from Divnogor'ye 9 is characterized by occlusal surfaces showing low relief and rounded or blunt cusps. It corresponds to mesowear scores comprised between values of 4–6, giving a high average mesowear score (MWS) of 5.0 and 5.1 in layers 5 and 6, respectively (Table 2). There is no significant difference between the mesowear scores from the two assemblages (Mann-Whitney *U* test; *U* = 76.5; *p* = .7481).

The mesowear scores fall in the range of extant grazers, and are slightly higher than those converted from the data published by Fortelius and Solounias (2000) for the extant *Equus quagga* (MWS = 4.7) and *Equus grevyi* (MWS = 4.5) (Fig. 3A). Such mesowear scores for the fossil horses from Divnogor'ye 9 indicate highly abrasive diets. In comparison to other fossil horse populations from Middle and Late Pleistocene sites in Western and Central Europe, the horses from Divnogor'ye 9 show the highest mesowear values (Fig. 3A). It should be noted that Divnogor'ye 9 mesowear scores partly overlap with the range reported at level F of Portel-Ouest (MIS 4–3, France).

The tooth microwear pattern of the horses from Layer 5 and 6 of Divnogor'ye 9 is characterized by a high number of scratches and relatively low number of pits (Table 2 and Fig. 4). The bivariate distribution of the numbers of pits and scratches (Fig. 5) as well as the %0–17 value (Fig. 3B) classifies the two populations among the extant grazers. In the two assemblages the gouges and cross scratches are absent (Table 2), the large pits are absent from the

Table 2

Summary of mesowear and microwear data for the fossil horse assemblages from Divnogor'ye 9 and other Pleistocene sites in Western Europe. Abbreviations: N = Number of specimens; MWS = Mesowear score; NP = Average number of pits; NS = Average number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = Scratch width score; %XS = Percentage of specimens with cross scratches; %0–17 = Percentage of specimens with number of scratches ranging between 0 and 17; M = Mean; SD = standard deviation; CV = coefficient of variation.

Site		Mesowear		Microwear							Reference	
		N	MWS	N	NP	NS	%LP	%G	SWS	%XS		%0–17
Divnogor'ye 9 layer 5	M	15	5.00	14	16.57	18.54	0	0	1.07	0	21.42	This study
	SD		0.65		3.69	1.75						
	CV		0.13		0.22	0.09						
Divnogor'ye 9 layer 6	M	11	5.09	11	16.00	19.14	9.09	0	1.18	0	18.18	This study
	SD		0.70		2.73	1.83						
	CV		0.14		0.17	0.10						
Schöningen 13 II-4	M	98	1.88	71	25.42	16.83	43.66	1.41	1.10	4.23	59.16	Rivals et al. (2015a)
	SD		1.17		7.68	4.64						
	CV		0.62		0.30	0.28						
Taubach	M	12	3.75	9	19.39	12.72	55.56	66.67	1.00	44.44	88.89	Rivals et al. (2009)
	SD		1.20		5.05	1.94						
	CV		0.32		0.26	0.15						
Wallertheim level F	M	14	2.93	13	22.96	28.08	53.84	53.84	0.53	7.69	0	Rivals et al. (2009)
	SD		1.49		5.60	2.87						
	CV		0.51		0.24	0.10						
Caune de l'Arago level G	M	37	3.92	38	8.34	32.82	7.89	5.26	0.16	8.16	0	Rivals et al. (2008)
	SD		1.36		2.22	5.70						
	CV		0.35		0.27	0.17						
Portel-Ouest level F	M	27	4.22	27	16.52	21.96	0	0	1.15	18.52	14.81	Rivals et al. (2009)
	SD		1.58		3.72	3.91						
	CV		0.37		0.23	0.18						

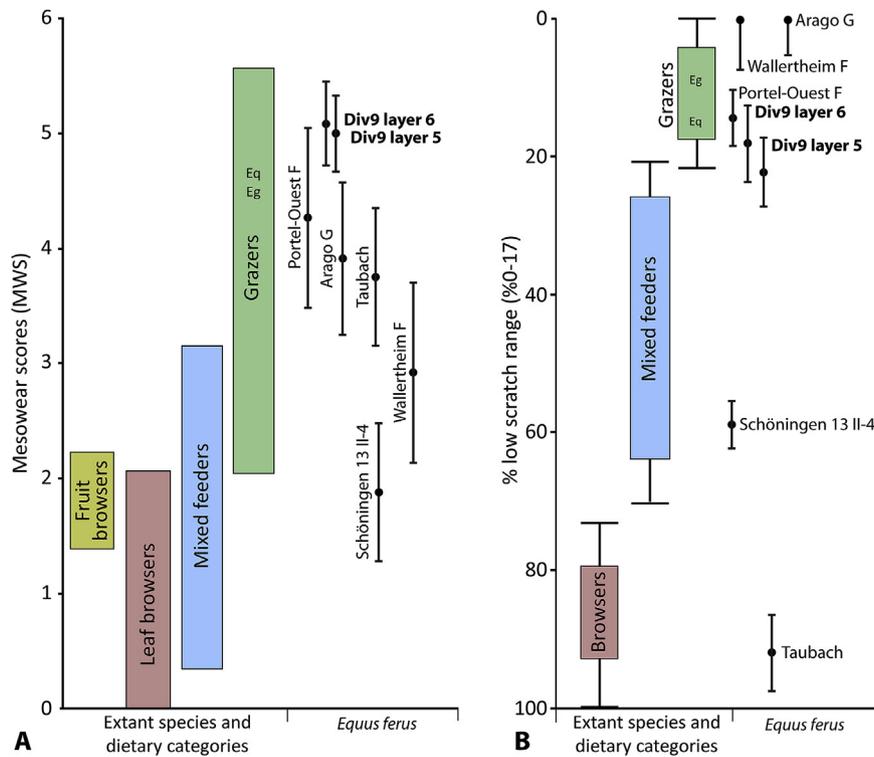


Fig. 3. Mesowear (A) and microwear (B) results for the ungulates from Divnigor'ye 9 (this study) and extant ungulates (from Fortelius and Solounias (2000), Solounias and Semperebon (2002), Rivals et al. (2010, 2014)). Abbreviations for extant equids: Eq = *Equus quagga*; Eg = *Equus grevyi*. Error bars correspond to standard deviation (± 1 SD) for the fossil samples.

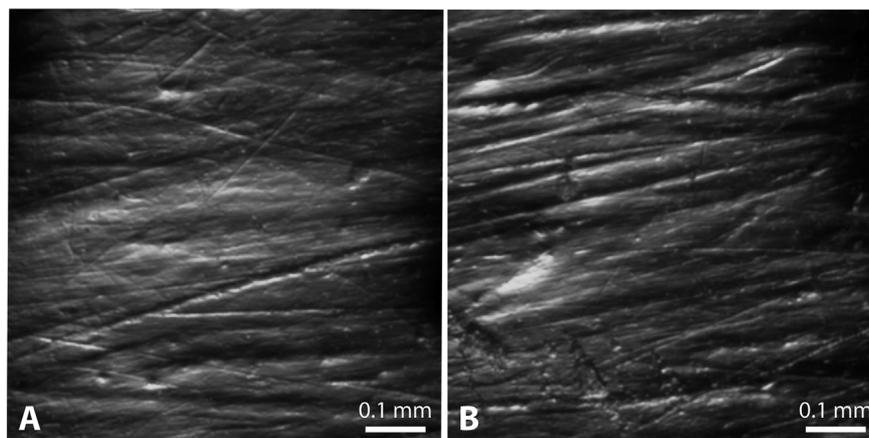


Fig. 4. Photomicrographs of selected fossil horse tooth enamel surfaces (35 \times magnification) from Divnigor'ye 9. (A) Right M2 (Specimen # 2015-135/59). (B) Left M2 (Specimen # 2009-35/297). Scale bar = 0.1 mm.

specimens from layer 5 and represent only a low percentage in layer 6. The scratches width score (SWS in Table 2) indicates a mixture of both fine and coarse scratches for the two assemblages. There is no significant difference between the two assemblages from layers 5 and 6, either in the number of scratches (Mann-Whitney U test; $U = 62$; $p = .4242$) or in the number of pits (Mann-Whitney U test; $U = 75$; $p = .9345$). The microwear pattern, with relatively high numbers of scratches (Figs. 3B and 5) also supports a grazing diet at the time of death for the horse in the two assemblages.

In comparison to modern equids (Fig. 5), the two samples from Divnigor'ye 9 are more similar to the extant Plains zebras (*Equus quagga*) which consume short and green grass (Grubb, 1981) than

to Grevy's zebras (*Equus grevyi*) which feeds on coarse and tougher-textured grasses and forbs (Churcher, 1993).

The results on the samples from Divnigor'ye 9 were compared to those published on other Pleistocene assemblages of horses from European sites. However, due to the scarcity of such studies on sites from the Late Glacial, the comparisons are made with sites from the Middle and Late Pleistocene (specifically from MIS 12 to 3). The two assemblages from Divnigor'ye 9 show consistent results with the two proxies, mesowear and microwear. The tooth wear pattern does not show any significant difference with the horse assemblage from Portel-Ouest level F, but is significantly different from those from Arago level G, Wallertheim level F, Taubach and Schönningen 13 II-4 (Figs. 3 and 5).

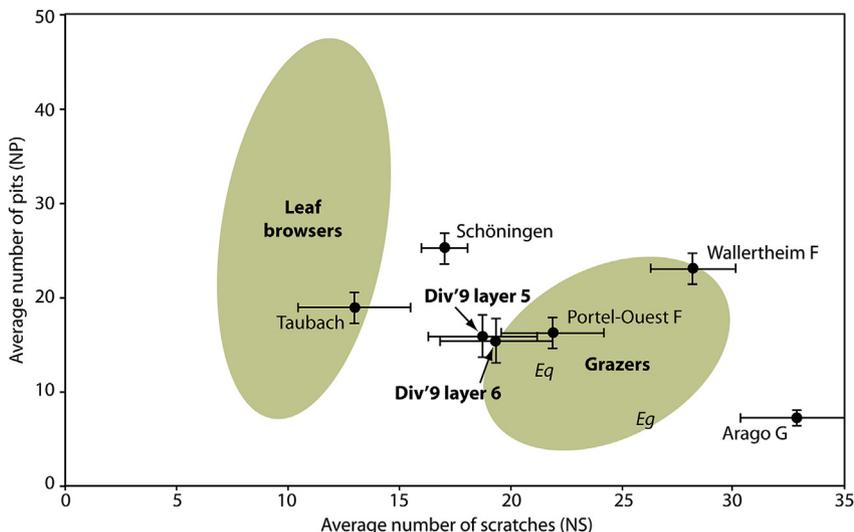


Fig. 5. Bivariate plot of the average numbers of pits and scratches in the fossil ungulates from Divnogor'ye 9. Error bars correspond to standard deviation (± 1 SD) for the fossil samples. Plain ellipses correspond to the Gaussian confidence ellipses ($p = .95$) on the centroid for the extant leaf browsers and grazers from Solounias and Semperebon (2002). Eq and Eg represent the modern zebras, *Equus quagga* and *Equus grevyi*, respectively.

4.2. Variability of the tooth microwear pattern and duration of accumulation

The two assemblages, layers 5 and 6, from Divnogor'ye 9 have low standard deviation (SD) and low coefficient of variation (CV) of the numbers of scratches (Table 2). In Fig. 6, these two samples plot in area [A] of the bivariate plot, indicating a short duration for the accumulation of the two assemblages. The formation of these two assemblages could have occurred in a single seasonal event or, more probably in a succession of events (at least two) at the same season over several years. Given the similar SD and CV values for the two assemblages, it is probable that each of these two assemblages were deposited during one or a succession of short event(s), i.e. a maximum of one season, and both assemblages would be attributed to the same season.

To verify this hypothesis, we computed the SD and CV values for

a “virtual” sample grouping the data from the specimens from layers 5 and 6. The resulting sample would plot in the area [A] if both occurred at the same season (e.g. both events in spring), in the area [B] if the two events are contiguous (e.g. one in spring and one in summer), in area [C] if they correspond to two non-contiguous events in time (e.g. one in spring and one in autumn). We obtained the following values, SD = 1.77; CV = 0.09. The resulting sample combining layers 5 and 6 plots in area [A], supporting our hypothesis that the events occurred at the same season of the year during the formation of the two layers.

In comparison to other sites from the Middle and Late Pleistocene, the duration of accumulation of the horse assemblages at Divnogor'ye 9 is significantly shorter than for the assemblages from Schönningen 13 II-4 (MIS 9, Germany) (Rivals et al., 2015a) or Portel-Ouest level F (MIS 4-3, France) (Rivals et al., 2015b), which were assigned to long-term events of accumulation (i.e. over more than a

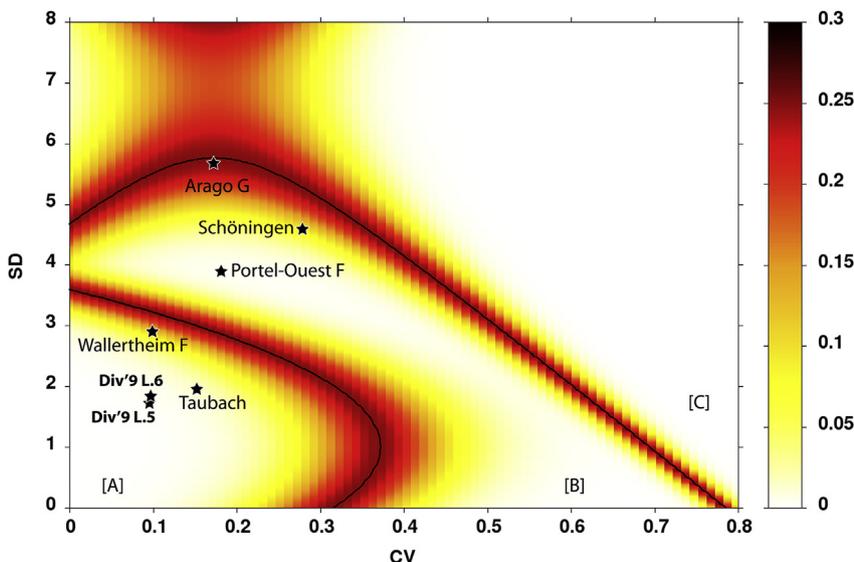


Fig. 6. Boundary lines with the error probability (heat map) based on SD and CV values of microwear data used for the classification of samples into short events (region A), long-term events (region B), or two separated short events (region C).

season), or to the succession of accumulation at different seasons. The two assemblages from Divnogor'ye 9 plot together with the horse assemblage from Taubach (MIS 5) which was identified as a short term occupation (Moncel and Rivals, 2011). Despite the chronological difference between these two sites, the microwear data indicate the same pattern of seasonal accumulation(s).

5. Discussion

5.1. Diet and habitat of the horse populations from Divnogor'ye 9

According to the mesowear and microwear signatures, the horse populations from Divnogor'ye 9 layers 5 and 6 were definite grazers. The mesowear value is one of the highest recorded for Middle and Late Pleistocene horses in Europe (Fig. 3). This confirms that grass was a strong component in the Divnogor'ye 9 horse diet, as reported by the stable isotopic data (see above, Table 1).

Grazing is the most common dietary signal observed among Middle and Late Pleistocene horses in Eurasia as well as extant equid species (Rivals et al., 2009, 2010; Schulz and Kaiser, 2013; van Asperen, 2010). However, both fossil and extant equids were found to show significant intraspecific variability related to habitats and resource availability (Rivals et al., 2009; Schulz and Kaiser, 2013). In the Pleistocene fossil record, various horse assemblages had a diet characterized by leaf browsing or browse-dominated mixed feeding, such as at Taubach (MIS 5) or Schöningen (MIS 9) in Germany (Rivals et al., 2009, 2015a). At Divnogor'ye 9, the dietary traits of the horse are very similar (both from micro and mesowear) to the horse from Portel-Ouest (level F, MIS 4–3) in southern France. The fauna from Portel-Ouest (level F) reveal humid and cold conditions, where the landscape was dominated by open habitats with availability of both grass and browse (Marquet et al., 1998). In similar conditions, where grass and browse were present in the landscape, horses were found to be grazers (Rivals et al., 2009).

Grazing is often associated with open habitats such as grasslands/steppes. However, grasses are also available in mixed habitats together with herbaceous plants, shrubs and trees. The pollen record of the lacustrine sediment at Divnogor'ye 9 indicates that grasses and dwarf shrubs including *Artemisia* and *Chenopodiaceae* were common while pine was the dominant tree species (Lavrushin et al., 2011; Sycheva et al., 2016). Therefore, the horse populations around Divnogor'ye 9 were likely living in habitats where both grass and browse were available but they were selectively, and exclusively feeding on grass as attested by their very high mesowear scores.

5.2. Repeated human occupations at Divnogor'ye 9

The site formation and the nature of human activity at Divnogor'ye 9 are still highly debated. Various hypotheses were proposed to explain the accumulation of the horses: a place for periodic mass killing and primary butchering of horses (Bessudnov and Bessudnov, 2010; Bessudnov et al., 2012, 2013), a natural accumulation resulting from repeated mudflows that caused the death of horses (Lavrushin et al., 2010, 2011), or a natural death of the horses at the end of winter or early spring followed by an accumulation of the remains by temporary flows to the entrance of the ravine (Kuznetsova et al. (submitted)).

Based on the site stratigraphy and the character of the cultural layers, there are no evidence of long distance movements of the archaeological remains downslope. The lacustrine sediments from Divnogor'ye 9 yielded multileveled accumulations of horse bones, often including almost complete skeletons, while flint artefacts are present in a limited quantity (Bessudnov et al., 2012; Bessudnov and Bessudnov, 2012). Both the lithic and the faunal remains

show signs that the assemblages are in primary position, this includes: lithic refits (including small flakes), good state of preservation of the lithic remains, excellent bone surface preservation, numerous anatomical connections, and absence of gnawing or trampling marks. There is also clear evidence of carcass processing, as confirmed by the presence of cut-marks on the bones and by the use-wear studies of the stone tools. The relatively small lithic assemblage with a high proportion of retouched tools - comprising more than 25% of the entire assemblage - is another signature of kill and butchery sites (Hoffecker et al., 2010). These elements suggest that Divnogor'ye 9 was likely a place where hunters practiced repeated killing and butchery of horse herds (Bessudnov et al., 2012; Bessudnov and Bessudnov, 2012; Kitagawa et al., in press).

The analysis of the variability of the tooth microwear pattern suggests that the site was repeatedly occupied during the same season over several occupational events (levels 5 and 6 studied here). From the tooth wear, it is impossible however to determine if these repeated events occurred during a single and unique season or during the same season over several years. The multidisciplinary study of the site also supports our results. The non-simultaneous formation of the two cultural layers is confirmed by a series of radiocarbon dates, as the series of AMS-dates (Lavrushin et al., 2011) obtained became consistently older from the upper layer to the lower one (with the exception for the layer 4). The low variability of the microwear patterns from adult teeth, clearly indicates that layers 5 and 6 are discrete layers but were occupied in the same season. According to the degree of fusion of the epiphysis and tooth wear of young individuals, the horses likely died in spring/summer in both layers and possibly in fall/winter in layer 5 (Bessudnov et al., 2013). This lends support to a scenario whereby humans visited the area over at least two separate periods (materialized as two layers) in the same season for hunting and is better explained as an accumulation resulting from mass killing of the horses by Late Glacial hunters. This meets the criteria for mass procurement established by Lubinski (2013).

Similar evidence is reported in the Late Paleolithic record such as in the early Upper Paleolithic open-air sites at Kostenki, located about 50 km from Divnogor'ye 9 on the west bank of the Don River, where large numbers of horses and reindeer were recovered (Hoffecker et al., 2010). In the Eastern Ukraine the Epigravettian site of Amvrosievka also points for the repeated use of a natural trap for hunting steppe bison in large numbers (Krotova and Belan, 1993; Julien, 2009; Krotova, 2013). In contrast, other sites previously identified as mass-kill accumulation have been reinterpreted, such as the Magdalenian site of Solutré (France) where the large number of horses, reindeer and bison were likely hunted during various seasons throughout the year (Turner, 2002). We found similar evidence at the Middle Pleistocene site of Schöningen (MIS 9, Germany) where the horses bone bed was found to be the result of an accumulation of events that occurred at different seasons (Julien et al., 2015; Rivals et al., 2015a).

6. Conclusion

The integrated analyses of tooth mesowear and microwear, combined with results from stable isotopes, zooarchaeology, and pollen analysis of the site permitted us to characterize the diet and environment of the horse populations around Divnogor'ye 9, but the most significant result is related to the nature of the accumulation of the horse remains at the site. Lines of evidence for mass-kills are difficult to provide in archaeological sites, and identifying single mortality event is a particularly challenging task. Using the non-destructive method of tooth microwear, we were able to identify a seasonal pattern in the procurement of the horse at Divnogor'ye 9 in at least two events represented by layers 5 and 6

respectively. This strengthens the model that hunter-gatherers were the agent responsible for the accumulation of the equid remains and further our understanding of mass kill events. In the future, we would like to apply high-resolution stable isotopic study to clarify the possible seasonality that the tooth wear data represent and to obtain a better understanding of the behaviors of the Late Glacial hunters and their preys in the steppe region of the northern latitudes.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.quaint.2018.01.008>.

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