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1 ***Title: Reindeer Feeding ecology and Hunting strategies by Magdalenians from Pincevent***
2 ***(Paris Basin, France): New Insights from Dental Microwear Textural Analyses.***

3
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5
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9
10 Abstract:

11 *In Pincevent (Paris Basin), archaeozoologists have observed a variation of hunting*
12 *strategies between Magdalenian levels IV0 and IV20. Previous works on human-prey*
13 *interaction showed that hunters modeled their behavior on their prey; therefore, reconstructing*
14 *animal behavior in order to reconstruct human strategies could enable better interpretation of*
15 *these levels. This study aims to contribute to a global understanding of the variation between*
16 *these level's hunting strategies using microwear texture analysis. This proxy, which can be*
17 *used to reconstruct diet, will enable to detect changes in the behavior pattern of the prey. The*
18 *decision was made to focus this study on reindeer (Rangifer tarandus) as it was one of the two*
19 *most exploited resources on this site, alongside horses. The enamel surface of teeth from two*
20 *populations of reindeer, hunted and found in levels IV0 and IV20, showed a variation of diet*
21 *between levels. Environmental and ecological matters are discussed with an aim to*
22 *understanding this variation of behavior in reindeer populations and highlight a change of*
23 *strategic behavior among hunters.*

24
25 Keywords: Reindeer, Pincevent, Paris Basin, Upper Magdalenian, Dental Microwear Textural
26 Analyses, Animal exploitation.

28

29 **1- INTRODUCTION**

30 The Paris Basin is a privileged region to study Magdalenian societies at the end of the
31 Paleolithic period (Late Glacial, 13,000–12,000 years BP; Figure 1A and Table 1). Among
32 the sites of this region, Pincevent occupation floors are a reference for exploring variations
33 over a very short time period due to its well-preserved stratigraphic sequence, resulting from
34 several overflows of silt or sandy silt from the Seine deposits (Figure 1b; Orliac 2006, 2014).
35 Based on archeological remains, paleo-ethnology studies were developed in Pincevent to
36 study Magdalenian occupations and reconstruct their way of life, their activities and their
37 social organization, all of which were linked to their subsistence strategies (Leroi-Gourhan &
38 Brézillon, 1966; 1972; Julien & Karlin, 2014). The huge number of faunal remains from
39 reindeer (*Rangifer tarandus*) and horses (*Equus caballus arcelini s.l.*, Bignon *et al.*, 2006), in
40 almost every level at Pincevent, and in many other sites of the region, indicates that the
41 Magdalenian economy was based on these two key prey (David, 1994; Enloe, 1998; Bignon,
42 2008; David *et al.*, 2014). This research underlines a coevolutionary link between prey–species
43 and prehistoric hunters during the Late Glacial in the Paris Basin (Bignon-Lau, 2014).

44 Dental microwear texture analysis was applied to assess the dietary spectrum of
45 Pincevent’s reindeer, in order to support hunting strategy changes and, most notably, the
46 season in which reindeer were most often slaughtered. As a ruminant, extant reindeer are
47 selective while their feeding behavior shows a relative plasticity. And they are described as
48 regional mixed feeder whose food component varies spatially and seasonally (Leader-
49 Williams, 1988; Skogland, 1984, 1989; Syroechkovskii, 1995; Semprebon and Solounias,
50 2002; Danell *et al.*, 2006): from lichen consumption throughout the year to other resources
51 depending on their availability in the environment (reconstructed by stomach content studies
52 ; Kuntz, 2011). During mastication, food items wear dental enamel, resulting in the so-called

53 dental microwear. When the animal dies, the dental microwear allows us to assess the food
54 properties of the animal from its last few days or weeks (Teaford et al, 1989a, 2017). When
55 applied to vegetarian species, diet mirrors vegetal resource availability, which highlights
56 habitat condition (Merceron et al., 2010).

57 Applied to a large range of species in the last 15 years, Dental microwear textural
58 analysis (Scott et al. 2005, Merceron et al. 2016, 2018) aims to assess differences in dietary
59 habits between inter- and intra-population scales (Percher et al. 2017; Berlioz et al. 2018;
60 Scott, 2012). Here, the method is applied on the archeological dental material from the two
61 levels excavated at Pincevent: level IV0 and level IV20. Each level is interpreted to
62 characterize a very distinctive faunal spectrum (Bignon *et al.*, 2006; Bignon, 2008; David *et*
63 *al.*, 2014; Bignon-Lau, 2014; Debout *et al.*, 2012): level IV20 represents a massive reindeer
64 killing in a single season (fall), whereas the level IV0 assemblages represent an association of
65 reindeer and horses hunted and killed over a period of approximatively a year.

66 With this paper, our main goal is to use this very rich and complex archaeological
67 grounds of these two exceptional preserved Magdalenian levels of Pincevent to show how
68 DMTA can bring relevant data highlighting both reindeer behavior and hunting strategies.
69 Two populations of present-day reindeer, with a total of 102 individuals living under different
70 habitat conditions in Norway, were used as comparative baselines (alpine tundra reindeer;
71 Bignon-Lau *et al.*, 2017).

72

73 **2- ARCHEOLOGICAL CONTEXTS**

74 ***2.1 - Magdalenian of the Paris Basin***

75 The Late Magdalenian (13,300–11,950 cal BC, Valentin, 2008; Debout *et al.*, 2011) is
76 currently the best-known period of the Pleistocene in the Paris Basin, with more than over
77 forty known sites. Most of these are highly concentrated in the south of Paris, in the Seine

78 Valley, with fewer settlement expansions in the northern and western zones of the region
79 (Figure 1a). Magdalenian sites provide some well-preserved occupations where the remains
80 are almost unaltered and found in their original position. For instance, the open-air sites of
81 Etiolles, Pincevent, Verberie and the sites of the Seine-Yonne confluence are stratified with
82 between five and fifteen occupation levels. These occupations are separated by thin deposits
83 of alluvia which have rapidly piled up due to the annual overflows of the River Seine. The
84 formation of these sequences is estimated to have occurred over a few generations, during an
85 instable climatic period, but it seems that the same individuals came back repeatedly (Bodu
86 2010; Julien and Karlin 2002; Rodriguez and Roblin-Jouve 2004). The successive return visits
87 to the same place confirm the regularity of displacements and allow functional variability of
88 the occupations within the same site to be studied. The environment around the sites has been
89 studied at sites such as Pincevent, Tureau-des-Gardes, Verberie, Etiolles, providing well-
90 preserved fauna remains.

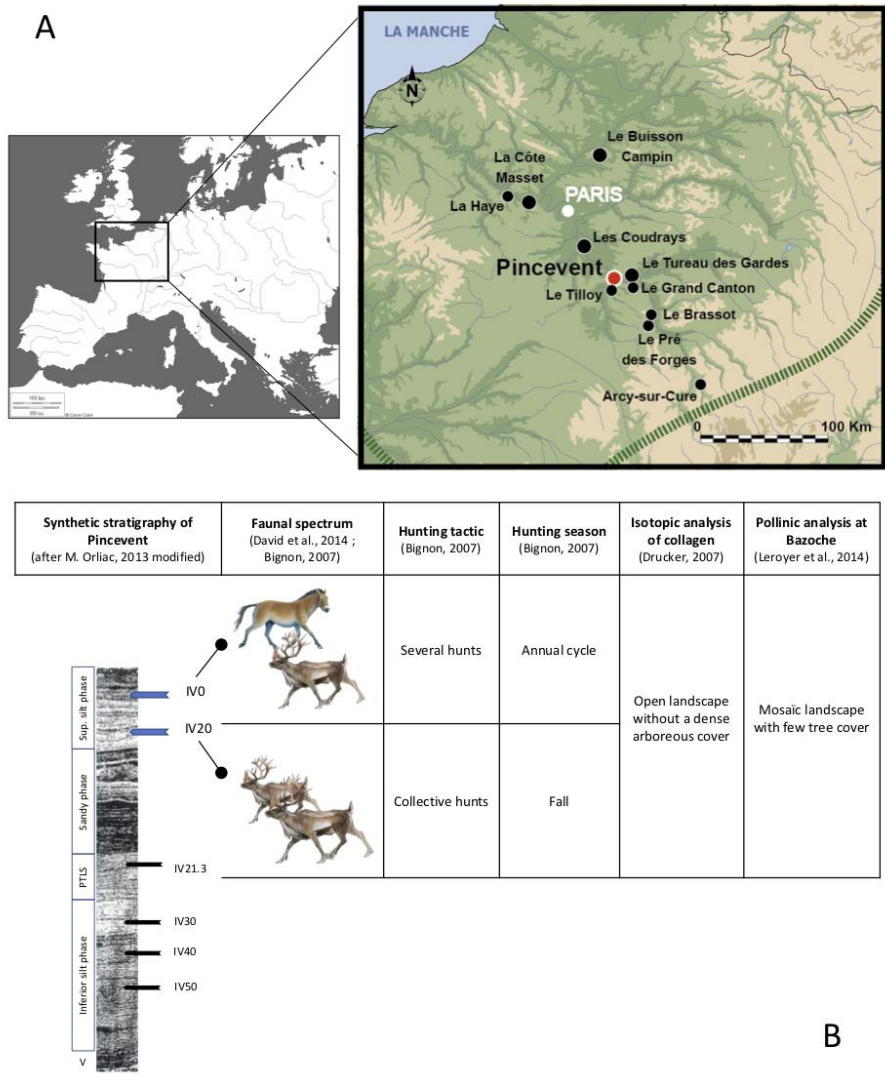
91 The Magdalenian sites were studied using the paleo-ethnographic approach elaborated
92 by André Leroi-Gourhan at Pincevent (Leroi-Gourhan and Brézillon 1966, 1972; see
93 Supplementary Information for details).

94

95 **2.2 - Pincevent**

96 Pincevent is an open-air site located in the middle Seine valley which offers very well
97 preserved archeological levels (Figure 1b). Among the Magdalenian sites of this region, it
98 remains a reference for exploring variations over a very short time period due to its well-
99 preserved stratigraphic sequence, covering at least one century (Figure 1b; Orliac, 2006).
100 Every year since its discovery in 1964, the site has been explored via the same planimetric
101 excavation method: every artifact is recorded on a square plan and in 3 dimensions, with
102 altitudes before removal. Today, this method is applied all over the world in open-air site

103 archeology. These meticulous excavation conditions allowed us to identify twenty-three
 104 occupation levels attributed to the Upper Magdalenian (Orliac, 1975; 2006; Ballinger *et al.*,
 105 2014).



106
 107 **Figure 1:** Map of Magdalenian sites of the Paris Basin (A) and environments and hunting season according to
 108 the hunting spectra in each stratigraphic level studied (B)
 109

110
 111 The two best-known levels on the site were excavated during several decades: level
 112 IV20 from 1967 to 1995, and level IV0 from 1989 to 2016. In each level of occupation, the
 113 synchronicity of the features is demonstrated by flint and heated stone refits that show a dense
 114 network of relationships (Bodu et al., 1993, 2014; SI, map of level IV20) and stratigraphic

115 control (Orliac, 2006, 2014).

116 All of the Magdalenian group occupations at Pincevent are attributed to the Upper
117 Magdalenian period between 14 000 and 11 800 calBC (Table 1; Valladas, 1994; Debout *et*
118 *al.*, 2012). The different occupations preserved in the overflow of silt from the Seine indicate
119 seasonal inputs of stream sediments (Roblin-Jouve, 1994), and the strength of the streams
120 suggest precipitations probably due to melting snow (Orliac, 1994). Grain size analysis of the
121 stratigraphic levels indicate environmental fluctuations linked to the Seine's watercourse
122 (Orliac, 2006; Bignon, 2008). These environmental oscillations seem to vary with the high
123 activity of the river, according to the seasons and other environmental factors (Bignon, *ibid*).

124

125 **Table 1:** *Dating Magdalenian levels IV20 and IV0 studied here*

126

127

Level	14C BP dates (*AMS)	CalBC dates	Nature of sample	Reference	Bibliography
IV20	12 120 ± 130	12 494-11 926	Charcoal	Gif 6283	Valladas (1994), p. 66
	12 600 ± 200*	13 407-12 551	Bone	OxA 148	Valladas (1994), p. 66
	12 250 ± 160*	12 860-12 072	Charcoal	OxA 467	Valladas (1994), p. 66
	12 450 ± 45*	13 082-12 456	Charcoal	ETH 37119	Bodu <i>et al.</i> (2009), p. 93
IV0	12 460 ± 70	13 084-12 202	Tooth	Lyon-9397	Orliac <i>et al.</i> (2013), p. 77
	12 440 ± 60	13 053-12 193	Bone	Lyon-9398	Orliac <i>et al.</i> (2013), p. 77
	12 580 ± 60	13 228-12 293	Tooth	Lyon-9399	Orliac <i>et al.</i> (2013), p. 77

128

129 The Pincevent site is located upstream of a fluvial bottleneck corridor (Figure 1A). Such
130 location, providing constant water and large floodplains, could have favoured concentration
131 of megafauna not far from human occupation; within an ecological community, multiple
132 species of large mammals (especially large herbivores) can coexist in a mosaic landscape
133 (Guthrie, 1982). And the simultaneous occurrence of reindeer and horse in the faunal
134 spectrum in Pincevent emphasizes the scenario presented by Bignon (2008). Indeed, there is

135 an alternation between two types of spectrum associating horses and reindeer (for instance in
136 level IV0) and the favoring of one species (mass killing of reindeer on level IV20; Enloe et
137 David, 2014; Bignon, 2007; Bignon-Lau, 2014). The site of Pincevent presents these two
138 types of hunting spectrum, which is why it is interesting to focus on this site to interpret the
139 change of tactics from a precise point of view.

140 Reconstructing the diet of the reindeer killed and consumed in Pincevent was applied
141 to the two most studied levels (IV0 and IV20), reflecting two hunting strategies. As they were
142 most likely hunted either all year round or targeted in a single short time span, and as their
143 dental microwear textures result from the mastication of the food items (and possibly
144 exogeneous particles ingested), we may expect differences between reindeer samples from
145 IV20 and IV0 levels.

146

147 Level IV20 was a short-term occupation of Magdalenians in Pincevent (see SI). The
148 predominance of reindeer (*Rangifer tarandus*) was attested by 98% of the total amount of
149 bones identified (4,542 bones, David *et al.*, 2014). Identification and ageing of these cervids
150 show a mortality profile very close of natural populations even if 3-5 years old adults seems
151 slightly overrepresented as well as male vs female adults (respectively 58 vs 42 %, considering
152 morphometric data). Moreover, the amount of reindeer found at this level (MNI = 76 -
153 Minimum Number of Individual - Table 2; Enloe & David, 2014), is likely to have been the
154 result of one or a very few massive hunting episode(s). Such hunting activities happened
155 during a very short window of time, in early fall, considering a set of considerations (David
156 *et al.*, 2014):

- 157 - this seasonality is consistent with observations of teeth composition and wear
158 (eruption rate of juveniles; Miller, 1974; Enloe & David, 2014);
- 159 - no foetal or new born bones have been found, indicating winter or spring occupations;

160 - only antler from hunted animals, both males and females were found (no shed ones),
 161 meaning that these specimens were killed between summer and early winter periods;
 162 however, only fall migration can provide such massive fusion of smallest male or
 163 female bands.

164 Besides these archaeozoological arguments, it has been established that the lithic production
 165 reflects an occupation lasting no more than two or three weeks (Julien, Karlin, 2014); such
 166 estimation of duration is in agreement with the clear spatial organization of units showing a
 167 few rates of rearrangements (areas of specialized work, toss zones, cleaning processes, etc.).
 168 Considering the whole set of archaeological data, the Magdalenian occupation of the level
 169 IV20 has been interpreted as a residential camp set up at a reindeer fall migration route,
 170 exhibiting a massive interception of such animal resource. We expect DMTA (Dental
 171 Microwear Texture Analysis) to characterize feeding ecology of reindeer at this period of the
 172 year.

173 **Table 2:** Faunal and other remains' data for IV20 and IV0 levels in Pincevent (locus regrouped)
 174

		Occupation level	IV20	IV0
Fauna		Excavated surface (m ²)	4 500	1500
		NR	4 643	22 076
		NRD	4 600	2 870
	NR (%)	<i>Rangifer</i>	98	63.13
		<i>Equus</i>	0.8	32.27
	MNI	<i>Rangifer</i>	76	46
<i>Equus</i>		2	34	
Heated stone		NR		13 000
		Weight total (tonnes)		1.5
Ornament		NR		298
		Shells (NR)		270
Lithic remains		NR	30 000/4 500 m ²	18 000/1 400 m ²

175
 176
 177
 178
 179

180 **Table 3:** *Taphonomy of level IV0 and IV20 – weathering (from A.K. Behrensmeyer, 1978) and destruction of the*
 181 *surface of the bone by the roots (B) – in David et al., 2014 p.79.*
 182

	Taphonomy	IV0 (%)	IV20 (%)
183			
184			
185		1	3.96
186		2	11.08
187	(A)	3	54.59
188		4	25.88
189		5	4.49
190		1	3.09
191	(B)	2	3.92
		3	6.53
		4	86.46

192 Level IV0 represents the very last Magdalenian occupation preserved at Pincevent
 193 (Bodu *et al.*, 2006). According to the sandy silt count from that level, there is around twenty
 194 year difference between the occupation of level IV20 and the occupation of level IV0, which
 195 is slightly inferior to the radiocarbon dating resolution for the Paleolithic period (Orliac, 2006
 196 ; 2014). At this level, the camp seems to have been, uncommonly, heavily structured by heated
 197 stones. This partially excavated camp was organized according to four units linked by refits
 198 of heated stones and/or lithic productions (Bodu, 2013). Unit 43-T125 was published in 2006
 199 and the recent work on all units (35-M103, 35-D110 and 25-V97) will be published in a
 200 monography currently in preparation (pers. com.).

201 In some localized parts of the level (20–30 cm under the surface), low and localized
 202 bioturbation is due to vegetation and burrowing animals (Table 3). Despite this situation, the
 203 occupation repartition and bioturbations did not impede economical interpretations
 204 concerning Magdalenian choices. With an almost equal amount of reindeer and horse remains
 205 (Reindeer: MNI = 43; Horses: MNI = 33, Table 2), hunting strategies were most likely
 206 different. The occupation on this level is typical of a “predominant association of horse-
 207 reindeer”: these two species represented almost 85% of the total number of remains (Table 2,
 208 Bignon, 2007; Bignon-Lau, 2014).

209 Seasonality indications were provided from teeth ageing (deciduous teeth vs
210 permanent teeth), dental crown height method and dental stage wear (Miller, 1974; crown-
211 height method; Bignon-Lau, 2006, 2007). In level IV0, it appears that the animals were killed
212 during multiple non-massive hunts throughout the year (Figure 1b). In contrast with
213 archaeozoological data in level IV0, the amount of lithic production is similar to level IV20.
214 This level shows a massive and entangled organization with numerous activities and phases
215 of waste disposal regrouped. Finally, it very likely seems that, a serie of multiple brief
216 occupations results in such seasonality data and the level IV0 spatial organization of remains
217 (Bodu et al., 2006; Debout, 2012).

218 We expect DMTA to reflect a largest variability of feeding habits and help us to
219 consider possibly a greater landscape image where happened these different hunting
220 strategies.

221 **3 – MATERIAL AND METHOD**

222 ***3.1 - Material***

223 We selected only teeth that presented an optimal enamel surface conservation, that is
224 similar at the scale of 3D scanning of surfaces to the ones of modern reindeer teeth. Faunal
225 remains from level IV20 were better preserved than those from level IV0 (Table 3), but in
226 accordance with our selection criteria, such different taphonomic contexts did not have any
227 effect on specimens analysed. However, more pronounced taphonomic alterations on level
228 IV0 lead to a much higher rate of rejected specimens. This greatest selection process from
229 level IV0 have been amplified because its MNI is smaller than from level IV20. For level IV0,
230 we selected 13 teeth from a total of 46 individuals (Bignon-Lau, 2019). For level IV20, 55 out
231 of 76 individuals (from sections 36 and 27; Julien & Karlin, 2014) were selected to be
232 analyzed.

233 Archeological samples were compared with two present-day populations of

234 Norwegian tundra adult reindeer from Knutshø (N=48) and Hardangervidda (N=54; Bignon-
235 Lau *et al.*, 2017), to interpret any intraspecific diet signal variations or mobility pattern
236 variations of regional population from present and past reindeer populations. The reindeer
237 populations in Knutshø and Hardangervidda belong to the Norwegian National Monitoring
238 Program for wild cervids. As part of this program, lower jaws are collected from animals shot
239 during the regular hunting season (the middle of August to the beginning of October).

240 **3.2 - Method**

241 DMTA was performed on disto-labial facets on the protoconid of lower molars (Figure
242 2A). Priority was given on M2 and complement was made with homologous dental facets on
243 third or first molars following Ramdarshan *et al.* (2017) recommendations.

244 Following standard procedures, teeth were cleaned and molded with a polyvinyl
245 siloxane (Coltène Whaledent, President Regular Body). Rather than producing a transparent
246 resin-based cast, the molds were scanned directly using the “TRIDENT” confocal surface
247 profilometer DCM8 Leica Microsystems, housed at the Palevoprim laboratory (CNRS-INEE
248 and the University of Poitiers). The profilometer was equipped with a 100× lens (Numerical
249 aperture = 0.90; working distance = 0.9 μm) and a 331 × 251 μm area was scanned for each
250 specimen. From this, four sub-adjacent surfaces (140 × 100 μm) were generated following
251 procedures shown in Berlioz *et al.* (2018), and pre-treated following Merceron *et al.* (2016)
252 and saved as Plμ files. The lateral sampling interval was 0.129 μm and the vertical spacing
253 was 0.002 μm. Further analyzes to generate DMTA variables were conducted with Toothfrax,
254 following procedures and settings provided by Scott *et al.* (2006).

255 Here, we focused on the four DMTA variables of the five detailed by Scott *et al.*
256 (2006): complexity (Asfc), anisotropy (epLsar) and heterogeneity of complexity (HASfc9 ;
257 Table 4; Scott 2012). Scott (2012) concludes that complexity (Asfc) is positively correlated
258 with the lignified tissues of woody vegetation, and negatively correlated to the amount of

259 abrasive (silica-bearing) monocots in a diet, whereas the anisotropy of the texture (epLsar) is
 260 positively correlated to the amount of tough vegetation such as grasses or mature tree leaves
 261 in the diet (see also Ungar *et al.*, 2007). According to previous studies on extant species and
 262 sheep raised and fed in captivity (Merceron *et al.*, 2014; Souron *et al.*, 2015; Ramdarshan &
 263 Merceron, 2016), the heterogeneity of complexity is positively correlated to the diversity of
 264 diet. Variations in dental microwear textures among the archeological and modern populations
 265 of reindeer were tested using Statistica software, by combining non-parametric Kruskal Wallis
 266 analysis of variances and post-hoc comparisons of mean ranks of all pairs of groups with a
 267 Bonferroni adjustment (Table 5).

268 **Table 4:** Textural data on levels studied at Pincevent.

Sites	n	Asfc			epLsarx10 ⁻³			HAsfc 9		
		mean	s.d.	s.e.m.	mean	s.d.	s.e.m.	mean	s.d.	s.e.m.
Level IV0	13	1.716	0.724	0.201	3.520	1.858	0.515	0.587	0.212	0.059
Level IV20	55	1.169	0.489	0.066	5.453	1.876	0.253	0.389	0.205	0.028
Hardangervidda	54	2.344	1.043	0.142	3.255	1.393	0.190	0.525	0.195	0.026
Knutshø	48	1.865	0.641	0.092	4.361	1.867	0.270	0.513	0.161	0.023

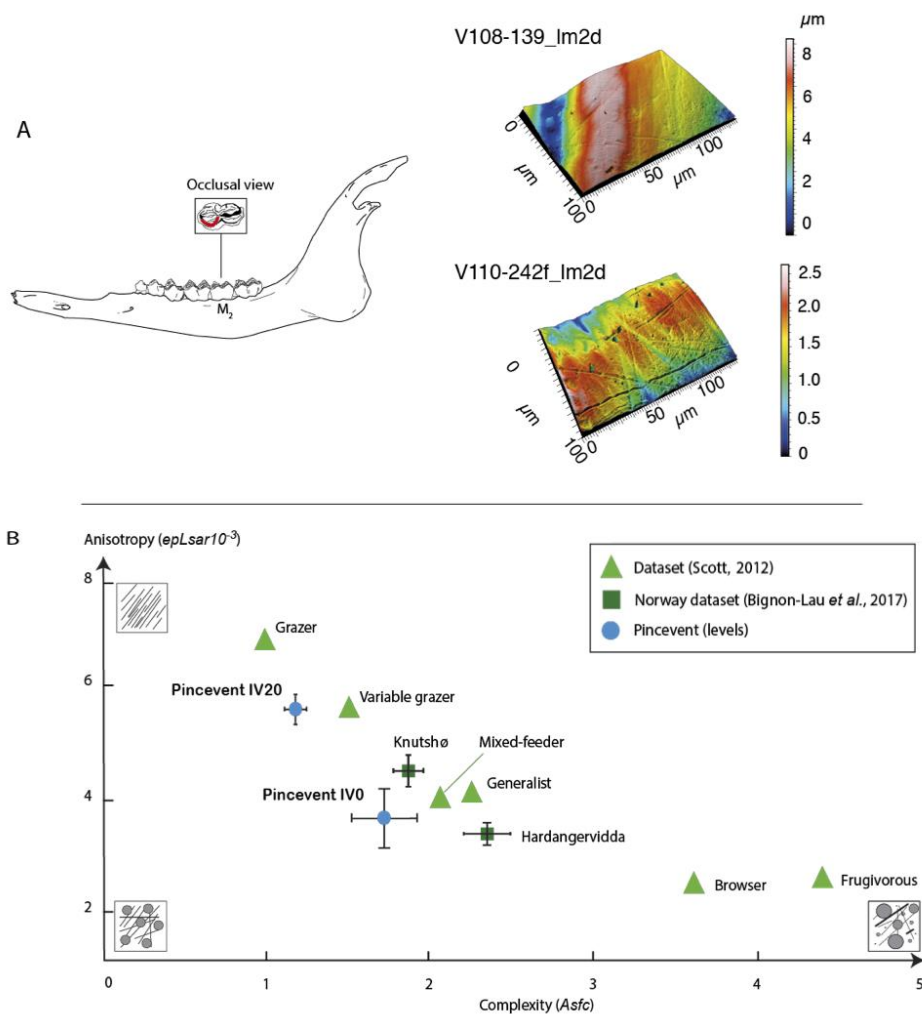
269 **Table 5:** Results of the non-parametric Kruskal Wallis analysis of variances and synthetic results of the post hoc
 270 multicomparisons test including reindeer from level IV20, level IV0 and the two Norwegian dataset (Knutshø and
 271 Hardangervidda).
 272

Variables	K	Df	p-value
<i>Asfc</i>	52.30433	3	< 0.0001
<i>epLsar</i>	34.86051	3	< 0.0001
<i>HAsfc₉</i>	29.47611	3	< 0.0001

	Hardangervidda	Knutshø	Level-IV0	Level-IV20
Hardangervidda				
Knutshø	epLsar			
Level-IV0				
Level-IV20	Asfc. epLsar. HAsfc ₉	Asfc. epLsar. HAsfc ₉	epLsar. HAsfc ₉	

277 **4 – RESULTS - Pincevent's reindeer diet**

278 The Kruskal-Wallis analysis of variance detected significant variations for all of the
 279 texture parameters (Table 4 and 5). The observed differences between the reindeer from the
 280 IV20 level and the two modern samples were all significant (Table 5, Figure 2). The reindeer
 281 from the level IV0 does not differ the modern population for any of the textural parameters.
 282 The reindeer from the IV20 level showed significantly higher value in anisotropy (epLsar)
 283 and lower one in heterogeneity of complexity (HAsfc9) compared with the cervids from level
 284 IV0 (Table 5, Figure 2).



285
 286 **Figure 2:** Sampling (in red) of an adult specimen (CAD - A. Lau-Bignon) (A), complexity in the anisotropy of
 287 dental microwear texture and diet of reindeer found in levels IV20 and IV0, with dataset from Scott, 2012 used as
 288 an illustrative reference (B).

289

290 5 - DISCUSSION

291 5.1. *Diet of reindeer and environments*

292 The dental microwear textures of the reindeer from level IV0 supported similarities in
293 dietary bolus with the two modern populations, which inhabit alpine tundra landscapes. Their
294 winter diet is dominated by lichens (62%), woody plants (16.3%), low percentages of mosses
295 (8.6%), and herbaceous monocotyledons (grasses, sedges, rushes; 6.3%, Skogland, 1984;
296 Bignon-Lau et al., 2017). However, these reindeer were slaughtered in late summer (from late
297 August till early October) a period during which the diet is more balanced with herbaceous
298 monocots (more than 45%), lichens (about 16%) and shrubs (11%) of the stomach content.
299 Bignon-Lau et al. (2017) have shown that the dental microwear textures of the two modern
300 populations of reindeer reflect these mixed feeding habits in late summer, although the
301 Knutshø population are more engaged in grazing in herbaceous monocotyledons than the
302 Hardangervidda samples. Differences in population density are most likely the main
303 parameter controlling the dietary spectrum; thus, explaining the differences in dental
304 microwear textures between the two populations. Due to a higher individual competition for
305 access to food resources, the individuals of the Hardangervidda population probably had to
306 enlarge their dietary spectrum to include more browsing and more lichens than the Knutshø
307 population. There is no doubt, therefore, that the reindeer from level IV0 were engaged in
308 both grazing and browsing.

309 The reindeer from level IV20 were significantly more engaged in grazing than the Knutshø
310 ones (Figure 2b). When plotting the reindeer data on the "complexity versus anisotropy"
311 continuum based on the African bovidea data (which are used as illustrative reference for
312 herbivores living in pasture ecosystem), Figure 2; Scott, 2012), the reindeer from level IV20
313 fell between variable and obligate grazers. Such dental microwear textures support either that
314 the food resources were abundant enough to provide full access to the preferred food

315 resources, or that the reindeer herds were not large enough to avoid individual competition for
316 food resources. Taking into account the archeological context, the former hypothesis seems
317 to be correct.

318 Paleoenvironmental reconstruction in the Paris Basin during the Late Glacial indicates a
319 mammoth steppe ecosystem, characterized by an association of communities of
320 megaherbivores and a mosaic landscape (Guthrie, 1982, 1984, 1990; Bignon, 2008). This is
321 confirmed by pollinic analyzes conducted in Bazoches-les-Brès, 5 kilometers from the
322 Pincevent site. The pollen spectrum attests to a steppic type of flora with a dominance of
323 herbaceous dicots (zone Baz a,b,c between 15 and 20% of *Rubiaceae* and *Compositae* ;
324 Leroyer *et al.*, 2014) and monocots (zone Baz a,b,c between 30 and 40% of *Poaceae* and
325 *Cyperaceae* ; Leroyer *et al.*, 2014). This is consistent with isotopic analysis conducted on
326 these regional sites which depicted an open environment without dense tree cover (tundra,
327 grasslands; Drucker, 2001). The herbivores found in the Paris Basin sites would have
328 frequented a tundra-like environment (with less lignified or semi-lignified shrubs and bushes,
329 however). They actually have higher $\delta^{13}\text{C}$ values of collagen than herbivores from dense tree
330 cover landscapes (Drucker, 2001). In the case of the IV0 and IV20 levels, reindeer “mean
331 values of $^{13}\text{C}_{\text{coll}}$ are set between -19.5 et -20.5 ‰” (Drucker, 2007; translated from French by
332 the authors, p. 251), indicating that they undoubtedly frequented an open environment.

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335 ***5.2. A shift in reindeer behavior***

337 In Pincevent, researchers generally tend to place the culling event of the IV20
338 occupation during the animals’ fall migration (mortality profile, sex-ratio, seasonal arguments,
339 short-term occupation indicated by low flint production and spatial organization), which
340 indicates that the herd was looking for more abundant food resources (David *et al.*, 2014). The
341 tactic developed by Magdalenian people at this time of year is consistent with the mortality

342 profile of a natural population: seasonal information (age of juveniles), the reindeer's MNI, as
343 well as the short duration of the camp (see SI for details; Julien, Karlin, 2014). Dental
344 microwear textural analyses of the IV20 reindeer show a strikingly narrow inter-individual
345 variability, an homogeneity that fits well with the short period of the fall culling event (Figure
346 2B).

347 On the contrary, less massive tactics were developed twenty years later during the IV0
348 occupation, with multiple hunting events occurring all year round. This yields a more complex
349 reindeer mortality profile (underrepresentation of juveniles, while young adults are
350 overrepresented) and denser units revealing the inner reorganization dynamics of the camp (SI;
351 Bodu *et al.*, 2006, 2011; Debout, 2012). We noted that the species targeted also changed: in
352 level IV20, reindeer represent almost all of the faunal spectrum, whereas level IV0 was shared
353 between reindeer and horses. When one is considering the largest period of reindeer hunts from
354 level IV0, embracing all seasons, it is not surprising to find a significantly greater inter-
355 individual variability of microwear values compared to level IV20 specimens (Figure 2b). In
356 addition, beyond the range of inter-individual diet variability we pointed out that there was no
357 significant overlap of the data (including standard deviation for $Asfc$ and $epLsarx10^{-3}$ in Figure
358 2b, table 4) between level IV20 and IV0. Though several reindeer were hunted in fall in both
359 levels (unit 43-T125 for level IV0; Debout *et al.*, 2006), the diet variability highlighted in this
360 paper was not restricted to cyclic seasonal fluctuations. These considerations, therefore, lead us
361 to consider that such targeted animals changed their feeding behavior during a short timespan
362 of twenty years.

363 ***5.3. Consequences and causes of changes in reindeer behavior***

364 From a Magdalenian hunter's point of view, such a significant shift in behavior concerning
365 one of their key-species was crucial for their whole settlement pattern and potentially for their
366 survival. We may hypothesize that resource availability influenced animal distribution and
367 density due to their movements or migrations (Skogland, 1989; Bennett, Provan, 2008;

368 Hopcraft *et al.*, 2010). In turn, reindeer availability and density all year round, or at some
369 predictable moments in case of migration, depends on hunting tactics, a collaborative amount
370 of people needed and the patterns of mobility of Magdalenian hunter-gatherers (Binford,
371 1978; Bignon, 2008; Julien, Karlin, 2014). In extant reindeer populations, we can observe
372 different type of migratory behavior. *Rangifer tarandus* can be sedentary when they are not
373 predated or live without demographic pressure, or can be generally sedentary-migratory when
374 only a part of the population is migratory (Reimers, 1983; Tyler and Oritsland, 1989; Geist,
375 1999; Loe et al., 2007; Kuntz, 2011). Migratory reindeer (entire herds) can cover very long
376 distance through winter or summer pastures.

377 Regarding resource availability, we know that abiotic factors (such as rainfall or soil
378 nutrients) can impact forage quality and abundance, resulting in herbivores of different sizes
379 (Hopcraft *et al.*, 2010). During the Magdalenian occupation, the environment was open but
380 fluctuations were registered during the Bölling period, according to sedimentology studies
381 (Orliac,2006). In fact, slight modifications of sediment composition occurred between the silt
382 deposit of IV20 level and the sandy silt deposit corresponding to IV0 level (Orliac,2006). The
383 latter sediment composition indicates slightly more force than the Seine, due to higher rainfall
384 or snowfall rates (Orliac,2006). Regarding such fluctuations, rain/snowfall variation are of
385 importance for plant's composition and abundance: reindeer could have been helped by
386 searching for more quality foraging. Would the paleoenvironmental conditions that could have
387 favored a shift in reindeer feeding behavior might also have led to migratory behavior?

388 Regarding level IV20, this very well preserved camp strongly suggests that the reindeer
389 were migrating (David et al, 2014). Conversely, the dental microwear texture of reindeer on
390 level IV0 is closer to the two Norwegian extant populations (Figure 2b, Table 5): different
391 seasons with different vegetal resources. We can therefore hypothesize that the reindeer from
392 level IV0 were less migratory than the reindeer from level IV20. But at this point, several

393 complementary analyzes (DMTA for broader spectrum of sites, and confrontation with intra-
394 tooth oxygen, carbon and strontium isotope variations) are needed to precise which scenario
395 could be the best one:

- 396 - level IV20 specimens were migratory but level IV0 ones were sedentary;
- 397 - level IV20 specimens were migratory but level IV0 ones became mixed sedentary-migratory
398 population;
- 399 - specimens of both levels were mixed sedentary-migratory populations and Magdalenian
400 changed their hunting tactics while reindeer got better physical condition.

401

402 **6 - CONCLUSION**

403 By analyzing the dental microwear texture of the 68 reindeer hunted by Magdalenians
404 and found in Pincevent, we have been able to identify variations of diet in reindeer between
405 levels IV0 and IV20. The signal provided complements those provided by the isotopic
406 analyzes of bone collagen applied on the same levels. Variability of reindeer behavior
407 suggests variability among hunting strategies during the Upper Paleolithic period. To
408 establish hunting strategies people must have gathered a thorough knowledge of reindeer
409 and horse ethology (migration paths, calving grounds). The hunters probably knew where to
410 find their prey, which is why reconstructing animal ethology with proxies, such as dental
411 microwear texture or isotopic analyzes, is important for reconstructing hunting strategies.
412 Reconstructing diet behavior in reindeer helped us define the Magdalenian's way of life in
413 the Paris Basin more precisely, and enabled the coevolution bond that persisted throughout
414 this period to be established.

415

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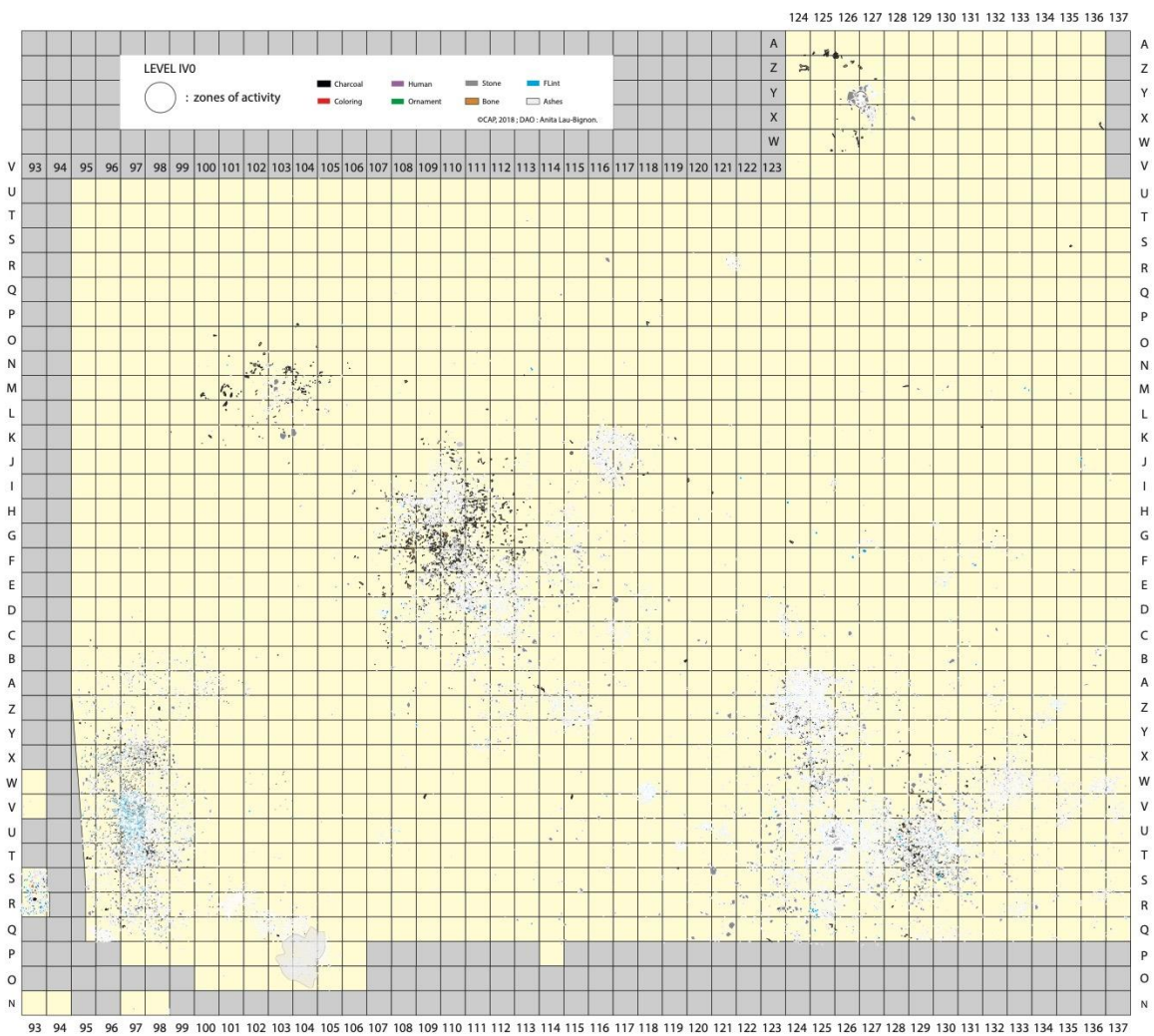
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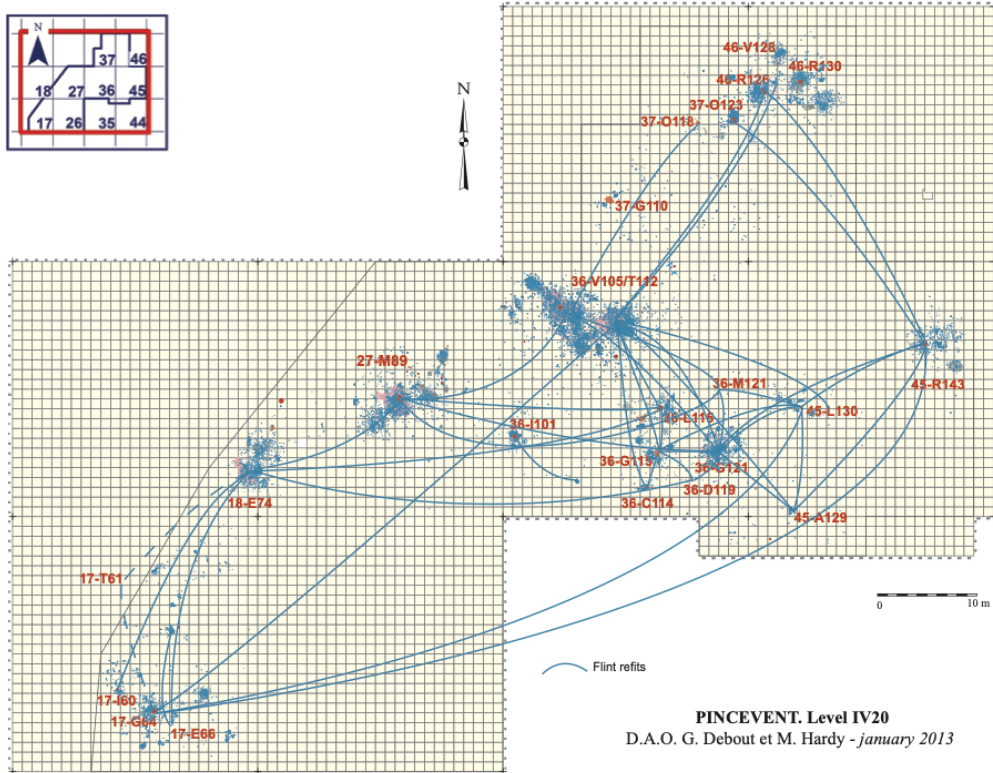
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