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The Last Glacial Maximum and the Late Glacial in northern France – Palaeoecological implications of animal community structuration and feeding behaviours based on dental microwear texture analysis

Le Dernier Maximum Glaciaire et le Tardiglaciaire dans le nord de la France – Implications paléoécologiques de la structuration des communautés animales et des comportements alimentaires d'après les analyses de texture des micro-usures dentaires

Das Letzte Glaziale Maximum und das Spätglazial in Nordfrankreich – Paläoökologische Schlussfolgerungen zu Strukturierung und Fressverhalten von Tiergemeinschaften anhand dentaler Mikrospuren-Texturanalyse

Olivier BIGNON-LAU, Natacha CATZ, Céline BEMILLI, Pierre BODU, Stephan HINGUANT, Jessica LACARRIÈRE, Gildas MERCERON, Cyril MONTOYA and Clément PARIS

Abstract: This paper examines the behaviour of animal communities in northern France from the Last Glacial Maximum (LGM) to the Late Glacial (LG). We explore how faunal remains can contribute significantly to a better understanding of the palaeoenvironment of the area that was a western hub between the southern and the northernmost European areas. Northern France is a crucial and fascinating geographical framework where animal communities survived extreme and unstable climate phases during the LGM and LG. More ample investigation is needed to understand such specific palaeoecological dynamics.

Based on the palaeoenvironmental context of specific animal communities, we focused on the composition variability of these communities in order to investigate their palaeoecological structuration and evolution. To complete our approach, we analyzed horse and reindeer dental microwear in order to characterize the feeding ecology of the prey most hunted by humans during both the LGM and

the LG in northern France. Based on our results, we would like to confront the models of Extension-Contraction and Cryptic Northern Refugia for the LGM, and evoke the evolution of colonization processes until the LG.

Keywords: Last Glacial Maximum, Late Glacial, Paris Basin, Animal community, Palaeoecology, Feeding behaviours.

Résumé : À la fin du Paléolithique, les périodes du Dernier Maximum Glaciaire (*Last Glacial Maximum*, LGM) et du Tardiglaciaire (*Late Glacial*, LG) sont traversées par de nombreuses oscillations climatiques, instaurant une instabilité environnementale. C'est d'autant plus le cas dans le Bassin parisien, en raison de ce positionnement géographique septentrional. Or les déplacements des espèces animales et des sociétés humaines, au cœur de nos problématiques, ne peuvent être dissociés dans l'évolution de ces systèmes complexes. Pour aborder les dynamiques de mobilité des sociétés humaines du Dernier Maximum Glaciaire et du Tardiglaciaire dans le Bassin parisien, nous avons opté d'examiner la mobilité de leurs ressources animales, selon deux échelles d'observation différentes et complémentaires. D'abord, à l'échelle des communautés animales et de leur évolution, il est intéressant d'observer la structuration des groupes d'espèces (régimes alimentaires, positionnements trophiques). Ensuite, à l'échelle spécifique, nous avons choisi d'étudier les comportements alimentaires du cheval et du renne (car chassés préférentiellement à nos périodes), à l'aide d'analyses texturales des micro-usures dentaires. Ces espèces représentent en outre des groupes distincts au sein des communautés animales : les équidés sont des monogastriques (herbivores généralistes), alors que les cervidés sont des ruminants plus spécialisés et aux besoins moins élevés quantitativement.

À l'échelle des communautés, nous avons pu vérifier la validité du concept de la « Steppe à Mammouth », élaboré par R. D. Guthrie (1982, 1984, 1990). Ce vaste biome, attesté sur la majeure partie du continent eurasiatique, semble bien avoir existé durant le LGM et le LG dans le Nord de la France. En témoignent les communautés végétales et animales très diversifiées que nous avons recensées, héritage d'une longue histoire évolutive commune. D'après la composition des communautés animales, nous serions bien en présence d'écosystèmes à pâturage, unis par de très fortes et anciennes interactions entre espèces animales et végétales. La diversité des herbivores traduit une partition des ressources végétales et de paysages hétérogènes ouverts, mais aussi une certaine diversité de carnivores de différentes tailles suggérant un haut degré de complexité des réseaux trophiques. Les communautés animales du LGM et du LG ne diffèrent que très peu entre elles dans le Bassin parisien. Cette similitude dans la structuration des peuplements ne signifie pourtant pas que ceux-ci aient eu le même fonctionnement paléoécologique (Bignon, 2008 et 2009 ; Bignon-Lau *et al.*, 2019). Dans les aires septentrionales de la France, nous devrions avoir une structuration écologique hétérogène des communautés, encore plus prononcée au LGM. Cet agencement impliquerait une abondance régionale variable des taxons et donc une densité spécifique fluctuante localement et/ou temporellement.

Pour analyser les comportements alimentaires du cheval et du renne, nous avons opté pour une approche multiscalaire, usuelle en biogéographie (Blondel, 1995) : (1) un niveau inter-individuel (échelle locale, une espèce, un site archéologique) ; (2) un niveau inter-populationnel (échelle régionale, une espèce et une période archéologique) ; (3) un niveau inter-spécifique, ici entre les rennes et les chevaux (échelle régionale/continentale, périodes LGM et LG) pour considérer à la fois de possibles tendances d'évolution et les relations interactives. En ce qui concerne l'analyse texturale des micro-usures dentaires, le principe est simple. Lorsque les plantes sont mastiquées par les animaux, elles marquent l'email dentaire et laissent des micro-usures. Ces micro-usures révèlent le régime alimentaire des derniers jours de la vie du spécimen étudié. Après avoir sélectionné, nettoyé et moulu une facette coupante dentaire, le moule est scanné avec un microscope confocal en lumière blanche (au laboratoire PALEVOPRIM, CNRS et université de Poitiers). On obtient un modèle 3D des surfaces dentaires qui seront analysées en fonction de paramètres de texture (Scott *et al.*, 2006), consistant en un calcul automatique, *via* des analyses fractales multi-échelles. Il est alors possible d'identifier par la sélection des plantes ingérées, les comportements alimentaires des herbivores et de reconstituer une part des habitats fréquentés par les animaux examinés. Ce faisant, nous avons des indications sur les lieux où les proies ont pu être abattues par les chasseurs.

Nos résultats montrent que les chevaux et les rennes du LGM et du LG ont consommé des ressources végétales, composées d'une bonne part d'herbacées monocotylédones (tendance à une forte anisotropie), mais aussi relativement variées. Il en ressort une image paléoenvironnementale cohérente avec à un paysage ouvert dominé de plaines steppiques. Ainsi, nos observations confirment les traits fondamentaux du modèle de Steppe à Mammouth, y compris pour le LGM. Cette période n'a rien d'un désert polaire, c'est aussi un écosystème à pâturage idéal à la fois pour les ruminants et pour les monogastriques, au moins à certaines périodes.

En ce qui concerne les rennes du LGM ou du LG, nous avons constaté des variations inter-individuelles relativement restreintes du régime alimentaire, mais les variations inter-populationnelles sont apparues plus marquées (entre herbivores intermédiaires et des païsseurs). En outre, les rennes de Pincevent ont connu des variations très rapides de comportement alimentaire entre différents niveaux d'occupation (Catz, 2016 ; Catz *et al.*, 2020). S'agissant des chevaux, à part à la grotte Rochefort, les spécimens de tous les sites LMG ou LG montrent une variabilité inter-individuelle plus importante par rapport aux rennes, se comportant en herbivores généralistes (avec parfois une tendance de païsseur). Au LG, les spécimens du niveau IV0 de Pincevent se rattachent aussi au pôle généraliste mais avec une tendance de brouteurs. Des travaux supplémentaires sont nécessaires pour établir s'il s'agit d'une évolution réelle dans le temps pour ces équidés. À l'échelle de la variabilité inter-spécifique (figs. 3, 4), nos résultats s'appuient en majeure partie sur les deux sites de la grotte Rochefort et de Pincevent (niveau IV0). Dans ces deux cas de figure, on peut entrevoir l'hypothèse d'une sélection dans le paysage de différentes franges d'une espèce à l'autre ou d'une relative partition des ressources. Ces résultats plaident en faveur d'une partition des ressources végétales.

Finalement, les analyses texturales de micro-usures dentaires permettent de mesurer la plasticité alimentaire des principaux herbivores paléolithiques. Ces études se poursuivent encore pour cerner la variabilité et l'évolution des comportements alimentaires, développées conjointement à des analyses isotopiques de la bioapatite (oxygène, carbone et strontium) sur spécimens actuels et archéologiques. L'analyse de la structuration des communautés alliée à celle des micro-usures dentaires illustrent les liens coévolutifs et la structuration des paysages. Enfin, nos résultats montrent que l'existence de refuges cryptiques septentrionaux au LGM dans le Nord de la France est plausible.

Mots-clés : Dernier Maximum Glaciaire, Tardiglaciaire, Bassin parisien, Communautés animales, Paléoécologie, Comportements de subsistances.

Zusammenfassung: In diesem Artikel wird das Verhalten von Tiergemeinschaften in Nordfrankreich vom Letzten Glazialen Maximum (LGM) bis zum Spätglazial (*Late Glacial*) untersucht. Wir erforschen, wie Faunenreste wesentlich zu einem besseren Verständnis der Paläoumwelt des Gebiets beitragen können, das ein westlicher Knotenpunkt zwischen den südlichen und nördlichsten Gebieten Europas war. Nordfrankreich stellt einen entscheidenden und faszinierenden geografischen Rahmen dar, in dem Tiergemeinschaften während des LGM und LG extreme und instabile Klimaphasen überstanden haben. Um diese spezifischen paläoökologischen Dynamiken zu verstehen, sind umfangreiche Untersuchungen erforderlich.

Basierend auf dem paläoökologischen Kontext bestimmter Tiergemeinschaften haben wir uns auf die Variabilität der Zusammensetzung dieser Gemeinschaften konzentriert, um ihre paläoökologische Strukturierung und Entwicklung zu untersuchen. Um unseren Ansatz zu verfolgen, analysierten wir die dentalen Mikrosuren von Pferden und Rentieren, um die Ernährungsökologie der meistgejagten Beutetiere des LGM und des LG in Nordfrankreich zu charakterisieren. Basierend auf unseren Ergebnissen möchten wir die Modelle der Extension und Kontraktion sowie der kryptischen nördlichen Refugien für das LGM gegenüberstellen und die Entwicklung der Kolonisationsprozesse bis zum Spätglazial aufzeigen.

Schlüsselwörter: Letztes Glaziales Maximum, Spätglazial, Pariser Becken, Tiergemeinschaften, Paläoökologie, Fressverhalten.

INTRODUCTION

AT THE END of the Palaeolithic, the Last Glacial Maximum (LGM) and the Late Glacial (LG) were marked by a series of climatic oscillations that most probably created multiple periods of environmental instability. This holds even truer for the Paris Basin and more generally the north of France: its northern geographic position may have contributed to the accentuation or acceleration of such changes. The spread and movement of animal species and human societies at the heart of our research cannot be dissociated from these complex ecological systems, within which they are nested at different levels. As Edgard Morin so elegantly stated,

‘[...] life cannot simply be atomized into organisms and compartmentalized into species: it also lives according to a self-eco-organisation. The evolution of life is also the evolution of ecosystems, in which the evolution of species is both the producer and the product’⁽¹⁾ (Morin, 1980, p. 89).

Our systemic perspective of faunal communities during the LGM and the LG in the Paris Basin is articulated around two different yet complementary scales of observation. On the one hand, we aim to consider the animal communities’ composition in order to characterize the balance between palaeoecologically functioning groups within a food web (especially generalist or monogastric herbivores; specialist herbivores or ruminants; omnivores; carnivores). Beyond biodiversity richness and the global structuration of landscapes, such considerations offer useful information concerning plant resource partitioning among animal species, a crucial element of palaeoecological research. Our arguments are consolidated and strengthened thanks to recent syntheses of available data, namely that such discoveries refute the conception of the Paris Basin as a ‘polar desert’ during the LGM.

On the other hand, it was also necessary to fine-tune the identification of the feeding habits of specific species.

This second scale sheds light on their ecological habitats, pinpointing which resources animals selected within these as well as the evolution of their choices. We focused on horses and reindeer as these two animal species are the most constantly recorded at our regional Upper Palaeolithic sites, and there are clearly more data on them than on other species. Moreover, these data are most regularly spread out over LGM and LG periods, which is useful when tracking behavioural changes. In addition, the two selected species belong to different groups of herbivores, thus hopefully highlighting certain features of their respective communities. Horses have large foraging requirements (as do other monogastrics, like the woolly mammoth and the woolly rhinoceros), and must adjust their needs to the available biomass and plants. Reindeer, however, are ruminants, like other cervids or large bovids, and behave more like selective herbivores, even if they are classified as mixed feeders considering the range of their fluctuating feeding habits (Dannell et al., 2006). The reconstruction of both species’ diets was achieved using dental microwear texture analyses.

Using our results to establish certain key ecological elements, we will discuss human mobility, which is clearly tied to available animal resources in such a palaeoenvironment. As horses and reindeer were systematically targeted by different prehistoric groups of the LGM and the LG in the Paris Basin, understanding how communities functioned and the different feeding behaviours of both species allowed us to better re-contextualise Palaeolithic hunting strategies. Defining the foraging areas of main preys also defines where hunts took place. Though such information is of great importance when considering modalities of acquisition (weaponry, hunting goals, supply logistics, etc.), the crucial motivator during the LGM and LG was finding food and a large range of animal raw materials (skins, tendons, antlers, etc.). Human settlement patterns in northern France during the LGM will be examined using the currently debated ‘Expansion-Contraction’ and ‘Cryptic Northern Refugia’ models.

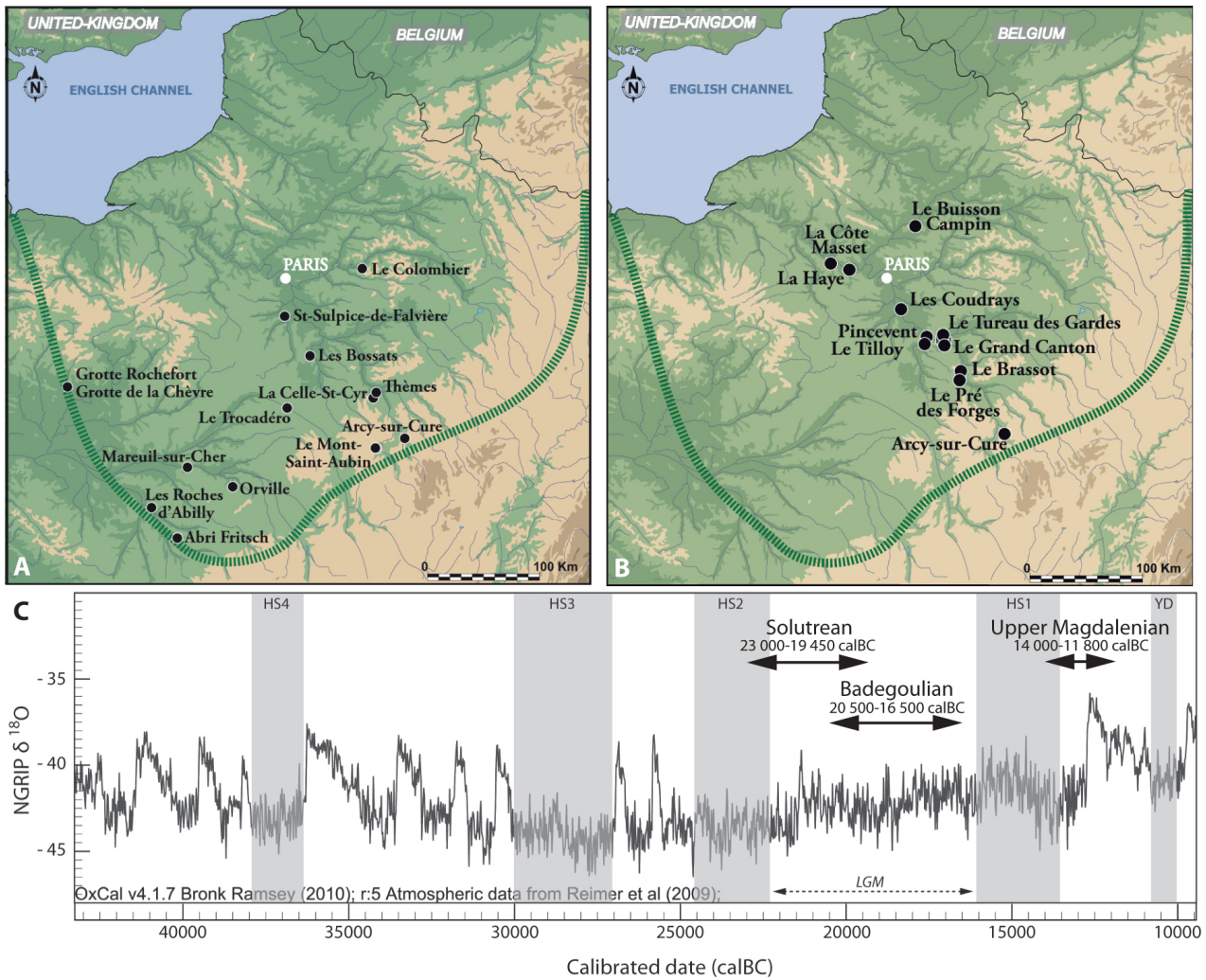


Fig. 1 – Distribution of (A) Badegoulian, Solutrean and (B) Magdalénian sites in the Paris Basin (the thick line corresponds to the geographic limit of the Paris Basin), (C) with their regional chronocultural periods of occurrence.

Fig. 1 – Répartition des sites (A) badegouliens, solutréens et (B) magdaléniens dans le Bassin parisien (la ligne large correspond à la limite géographique du Bassin parisien), (C) avec leurs périodes chronoculturelles régionales d'apparition.

Abb. 1 – Verteilung von (A) Badegoulien-, Solutréen- und (B) Magdalénien-Fundstellen im Pariser Becken (die dicke Linie stimmt mit der geographischen Grenze des Pariser Beckens überein), (C) mit ihren regionalen, chronokulturellen Perioden.

ENVIRONMENTAL CONTEXTS AND CULTURAL ENTITIES DURING THE LGM/LG

The evolution of climate conditions

The LGM is known as a period of intense cold between 20,000 and 15,000 years BP (21,500 and 16,500 calBC), during which the Scandinavian glaciers extended most rapidly around 20,500 years calBC (Mix et al., 2001; Clark and Mix, 2002; Blockley et al., 2012). Chronologically, the LGM was flanked by the H1 and 2 Heinrich periods, considered to be even more intense glacial periods (fig. 1).

During the LGM, the maximum extension of glaciers led to an extreme drop in sea levels (Mix et al., 2001; Clark and Mix, 2002; Blockley et al., 2012). Dependent on climate variations, the estimated winter temperatures in the immediate vicinity of the glaciers lay between -40

and -20°C, and probably rose to barely above freezing in summer (Mix et al., 2001; Prud'Homme et al., 2016). As a result, throughout the Paris Basin, seasonal differences were more marked due to a more continental geographic configuration (fig. 1). A portion of northern France endured strong winds, bringing thick loess deposits, at the heart of which several layers of tundra gley have been found, attesting to brief episodes of warmer weather (Antoine et al., 2009; Moine et al., 2011; Prud'Homme et al., 2015; Antoine et al., 2016). In addition to these regional climate fluctuations, a geographic variability in temperatures linked to local characteristics may have existed according to certain models (Svenning and Skog, 2007).

The LG period consists of contrasted climate phases, as illustrated in the division of palynological chronozones (Dryas I, Bølling, Dryas II, Allerød, Dryas III) that are connected to a number of environmental upheavals (Magny, 1995). The Dryas I was an extremely

cold period (around 15,000 BP; 16,500 calBC) that has now been determined as corresponding to the H1 event. Then, a sharp rise in temperatures ushered in the Bølling (towards 12,700 BP; Björck et al., 1998): this chronozone was characterized by a highly unstable climate, marked by a great amplitude in oscillations, followed by a sharp cooling phase that characterizes the Dryas II (roughly 12,000-11,800 BP). The following Allerød had a cool, humid climate that contrasted sharply with the return of glacial conditions during the Dryas III (roughly between 11,000 and 10,000 BP). It is generally accepted that the Bølling and Allerød constituted an interstadial period, in other words the initialisation of an aborted interglacial phase (Magny, *ibid.*).

Cultural characteristics of human societies of the LGM

A small number of deposits, not all of which have been dated, prove the presence of Solutrean groups in northern France (table 1). Traces of the earliest phase of the Solutrean/Proto Solutrean period are still rare and can only be found at the sites of the Trilobite cave in Arcy-sur-Cure, and Celle-Saint-Cyr, Yonne (Renard, 2002; Bodu and Renard, 2013; fig.1A). Middle and Late Solutrean remnants are more commonly identified throughout this geographic area: the caves in Rochefort (Hinguant and Biard, 2013; Biard and Hinguant, 2015), in Saint-Sulpice-de-Favières, in Ormesson (Sacchi et al., 1996; Bodu, 2014;

| Period | Site | Level/layer | ¹⁴ C date (*AMS) | Material | Lab. No | Reference |
|-------------|----------------------|--------------------|-----------------------------|----------|--------------------|--------------------------|
| Gravettian | Amiens-Renancourt 1 | - | 21 890 ± 90 | Bone | Beta-306063 | Paris et al., 2017 |
| Gravettian | Amiens-Renancourt 1 | - | 22360 ± 350 | Bone | OxA-7761-Ly-633 | Paris et al., 2017 |
| Gravettian | Amiens-Renancourt 1 | - | 23040 ± 220 | Bone | OxA-7654-Ly-632 | Paris et al., 2017 |
| Solutrean | Les Bossats Ormesson | Solutrean level | 19580 ± 110 | Charcoal | Ly-12620/SacA44273 | Bodu et al., 2019 |
| Solutrean | Grotte Rochefort | - | 15 220 ± 60 | Bone | GrA-38260 | Hinguant and Biard, 2013 |
| Solutrean | Grotte Rochefort | - | 18 395 ± 90 | Bone | GrA-1438 | Hinguant and Biard, 2013 |
| Solutrean | Grotte Rochefort | - | 19 025 ± 120 | Bone | GrA-38337 | Hinguant and Biard, 2013 |
| Solutrean | Grotte Rochefort | - | 19 190 ± 110 | Bone | GrA-38323 | Hinguant and Biard, 2013 |
| Solutrean | Grotte Rochefort | - | 19 500 ± 70 | Bone | GrA-38157 | Hinguant and Biard, 2013 |
| Solutrean | Grotte Rochefort | - | 19 600 ± 80 | Bone | GrA-38159 | Hinguant and Biard, 2013 |
| Solutrean | Grotte Rochefort | - | 19 490 ± 90 | Bone | GrA-34087 | Hinguant and Biard, 2013 |
| Solutrean | Grotte Rochefort | - | 19 320 ± 90 | Bone | GrA-34092 | Hinguant and Biard, 2013 |
| Solutrean | Grotte Rochefort | - | 19 590 ± 90 | Bone | GrA-34079 | Hinguant and Biard, 2013 |
| Badegoulian | Abri Fritsch | 3 (upper phase) | 17 130 ± 550 | Bone | Ly-1121 | Trotignon et al., 1984 |
| Badegoulian | Abri Fritsch | 4 (upper phase) | 16 530 ± 350 | Bone | Ly-1122 | Trotignon et al., 1984 |
| Badegoulian | Abri Fritsch | 5b (earlier phase) | 17 280 ± 350 | Bone | Ly-1123 | Trotignon et al., 1984 |
| Badegoulian | Abri Fritsch | 6 (earlier phase) | 17 960 ± 350 | Bone | Ly-1124 | Trotignon et al., 1984 |
| Solutrean | Abri Fritsch | 8d | 19 180 ± 230 | Bone | Gron-5499 | Trotignon et al., 1984 |
| Badegoulian | Le Colombier | - | 17 010 ± 60* | Charcoal | Beta-288449 | Montoya et al., 2019 |
| Badegoulian | Le Colombier | - | 17 200 ± 60* | Bone | Beta-288447 | Montoya et al., 2019 |
| Badegoulian | Le Colombier | - | 17 250 ± 70* | Bone | Beta-326596 | Montoya et al., 2019 |
| Badegoulian | Le Colombier | - | 18 030 ± 70 | Bone | Beta-326594 | Montoya et al., 2019 |
| Badegoulian | Le Colombier | - | 18 150 ± 70 | Charcoal | Beta-288448 | Montoya et al., 2019 |
| Badegoulian | Le Colombier | - | 18 570 ± 120 | Bone | Ly-8977 | Montoya et al., 2019 |
| Badegoulian | Le Colombier | - | 18 680 ± 150 | Tooth | Ly-5377 | Montoya et al., 2019 |
| Badegoulian | Le Colombier | - | 18 660 ± 140 | Tooth | Ly-6378 | Montoya et al., 2019 |
| Badegoulian | Le Colombier | - | 19 320 ± 110 | Tooth | Ly-8976 | Montoya et al., 2019 |
| Magdalenian | Les Coudrays | Q-R5 | 12 000 ± 220 | Bone | Ly-1351 | Valladas, 1994 |
| Magdalenian | Les Coudrays | N20 | 12 900 ± 300* | Bone | OxA-138 | Valladas, 1994 |
| Magdalenian | Les Coudrays | N20 | 13 000 ± 300* | Bone | OxA-139 | Valladas, 1994 |
| Magdalenian | Les Coudrays | N20 | 12 800 ± 220* | Bone | OxA-173 | Valladas, 1994 |
| Magdalenian | Les Coudrays | N20 | 12 900 ± 220* | Bone | OxA-175 | Valladas, 1994 |
| Magdalenian | Les Coudrays | A17 | 12 250 ± 100* | Bone | OxA-5995 | Olive, 2004 |
| Magdalenian | Les Coudrays | D71 | 12 315 ± 75* | Bone | OxA-8757 | Olive, 2004 |
| Magdalenian | Les Coudrays | Q31 | 12 315 ± 55* | Bone | OxA-12019 | Olive, 2004 |
| Magdalenian | Le Tureau des Gardes | TDG6 | 12 290 ± 90* | Bone | Ly-6988 | Bridault et al., 1997 |
| Magdalenian | Pincevent | IV20 | 12 120 ± 130 | Charcoal | Gif-6283 | Valladas, 1994 |
| Magdalenian | Pincevent | IV20 | 12 600 ± 200* | Bone | OxA-148 | Valladas, 1994 |
| Magdalenian | Pincevent | IV20 | 12 250 ± 160* | Charcoal | OxA-467 | Valladas, 1994 |
| Magdalenian | Pincevent | IV20 | 12 450 ± 45* | Charcoal | ETH-37119 | Bodu et al., 2009 |
| Magdalenian | Pincevent | IV213 | 12 400 ± 200* | Bone | OxA-149 | Valladas, 1994 |
| Magdalenian | Pincevent | IV213 | 12 000 ± 220* | Bone | OxA-176 | Valladas, 1994 |
| Magdalenian | Pincevent | IV0 | 12 300 ± 220* | Bone | OxA-177 | Valladas, 1994 |
| Magdalenian | Pincevent | IV0 | 12 460 ± 70 | Tooth | Ly-9397 | Orliac, 2013 |
| Magdalenian | Pincevent | IV0 | 12 440 ± 60 | Bone | Ly-9397 | Orliac, 2013 |
| Magdalenian | Pincevent | IV0 | 12 580 ± 60 | Tooth | Ly-9397 | Orliac, 2013 |

Table 1 – Lists of ¹⁴C dates for Paris Basin sites cited in this study.

Tableau 1 – Listes des dates radiocarbone du Bassin parisien cités dans l'étude.

Tabelle 1 – Liste mit ¹⁴C-Daten der Fundstellen im Pariser Becken, die in diesem Aufsatz aufgeführt werden.

Bodu et al., 2014 and 2019), in levels 7 to 10 of the Fritsch shelter (Allain, 1976 and 1978; Trotignon et al., 1984), and at Maitreaux (Aubry et al., 1998). Other discoveries testify to the presence of Solutrean groups in the Centre region and in the north of France (the Erve valley in Mayenne: Allard, 1983 and 1985; Hinguant and Colleter (eds.), 2020); more vague traces have been found in the Roches d'Abilly, the Monthaud shelter, Chalais, etc. (Pradel and Pradel, 1967; Agogu , 2005; Aubry et al., 2007).

Lithic production (or the associated facies, see Montoya et al., 2019), related to radiocarbon dates, confirms the presence of Badegoulian societies in the Paris Basin (fig. 1A). A few such sites are the Bois des Beauregards in Nemours (Bodu et al., 2007; Schmider and Roblin-Jouve, 2008), the Fritsch shelter (levels 3 to 6; Trotignon et al., 1984), and the Mont-Saint-Aubin in Oisy (Bodu et al., 2007; Debout et al., 2012). In addition, there are LGM sites without clear defined cultural characterisation such as Colombier in Ch zy-sur-Marne (Paris, 2011; Montoya, 2014), or the site of Th mes (Malgarini et al., 2017), possibly related to early phases of Lower Magdalenian. Here too, it is worth noting the existence of more modest clues, such as finds from the Grotte de la Ch vre (Hinguant and Biard, 2013), as well as in La Croix-de-Bagneux (Kildea et al., 2013), the Bois des Beauregard, the Trocad ro, and in Orville (Chehmana et al., 2007 and 2013; Malgarini et al., *ibid.*). Recent discoveries and the renewed analysis of industries over the past few years clearly indicate that northern France was occupied during many phases of the LGM.

During the LG, the oldest vestiges of Magdalenian settlement in the Paris Basin can be found in  tiolles (table 1, fig. 1B; Bodu et al., 2011; Debout et al., 2012 and 2014; Olive et al., 2019). There are over forty sites in the region, with faunal remains unevenly distributed across all of them (Bignon, 2003 and 2009). Certain, exceptionally well preserved open air deposits offer several layers of successive occupation (especially Les Coudrays- tiolles, Pincevent, Verberie). These sites are situated at the bottom of regularly flooded valleys, as is the case along the rivers Seine or the Oise; but other discoveries have been made in other contexts such as in the Loing valley (Schmider, 1992; Bodu et al., 2006; Pigeot, 2004; Enloe, 2010; Debout et al., 2011; Julien and Karlin, 2014).

Key preys hunted

With current data, it would seem that reindeer and horses were key preys throughout the Upper Palaeolithic in the Paris Basin, regardless of the cultural entity (Bignon-Lau, 2014). But, as proven for the Magdalenian of the Paris Basin (Bignon, 2007a and 2008), a different balance in hunting strategies can be found (table 2): predominantly reindeer, predominantly horses, or a joint preference for reindeer and horses. It is remarkable that this configuration of hunting choices during the LG is generally identical for older societies of the LGM in the region (Solutrean, Badegoulian, Lower Magdalenian).

As they were regularly hunted, we can conclude that the distribution of reindeer and horse populations were

relatively constant in the area, including during the LGM. The near exclusive presence of these two preys also allows us to infer other palaeoecological implications that we will touch upon later, notably the coevolutionary relationships between predator and prey. In addition, we will also focus on better understanding how human societies traveled and were organized during the LGM and the LG, by characterizing the mobility of their key preys.

Plant communities

Mainly due to preservation issues, palynological data alone are insufficiently reliable to allow us to recreate the plant communities in this type of context (Jackson and Williams, 2004; Feurdean et al., 2007; Binney et al., 2009). Over the past few years, the many analyses have thus preferred plant macro remains (charcoal), systematically dated, with results sometimes backed up by palaeogenetic analyses (Willis and Van Andel, 2004; Anderson et al., 2006; Magri et al., 2007; Magri, 2008 and 2010; Bhagwat and Willis, 2008; Kullman, 2008; Petit et al., 2008; Binney et al., 2009; Normand et al., 2011). Based on hundreds of sites and several thousand samples, results show the existence of relatively diversified varieties above the 40th parallel north at the scale of the Eurasian continent. Such research has contributed to renewing the picture of plant landscapes during the most critical glacier phases, notably during the LGM. It would seem that these plant communities can be qualified as 'non analogue'. This term indicates that these communities offer up associations of species that are atypical when compared to their modern day counterparts. During the LGM, plant communities appeared notably more diversified in their northern distribution. Based on previously cited research, the simulations of areas of distribution of various plant species during the LGM (Svenning et al., 2008) offer interesting conclusions. Thus, vast Nordic distributions that extended all the way to the ice caps seem plausible for the following trees: grey alder (*Alnus incana*), silver and white birch (*Betula pendula*; *B. pubescens*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), European aspen (*Populus tremula*), and goat or pussy willow (*Salix caprea*).

Thanks to a number of radiocarbon datings, it has been discovered the existence of a forest cover that was most likely heterogeneous, extending to within several kilometers of the glaciers, even during the LGM (Willis and van Andel, 2004; Kullman, 2008; Magri, 2010). In humid zones with less wind, certain deciduous trees sometimes managed to constitute small forests, alongside conifers, which were more common during the LGM. In western and central Europe, the tree layer also seems to have spread widely with variable densities depending on local configurations (Bhagwat and Willis, 2008; Svenning et al., 2008; Binney et al., 2009; Normand et al., 2011). Recent discoveries in the northern half of France, at the Rochefort cave (Mayenne) and in Ormesson (Seine-et-Marne), comply to this schema. Several types of charcoal were identified in the Solutrean levels 4.6 to 4.2 of

| Culture | Site/Number of Remains (NR) | Horse | Reindeer | Faunal spectrum type | References |
|-------------------------------|--|-------------------|----------------------|-----------------------------|--|
| Solutrean | Abri Fritsch - Level 9 (NR=2479) | NR=3 / MNIF=1 | NR=29 / MNIF=2 | Reindeer predominance | Bayle, 2000 |
| | Abri Fritsch - Level 8b (NR=5731) | NR=4 / MNIF=1 | NR=35 / MNIF=3 | Reindeer predominance | Bayle, 2000 |
| | Abri Fritsch - Level 7b (NR=2328) | NR=2 / MNIF=1 | NR=25 / MNIF=2 | Reindeer predominance | Bayle, 2000 |
| | Grotte Rochefort (NR=5500) | NR=306 / MNIF=8 | NR=475 / MNIF=15 | Reindeer/Horse predominance | Bemilli and Hinguant, 2014 |
| | Les Bossats Ormesson (NR=230) | NR=11 / MNIF=1 | NR=10 / MNIF=1 | Reindeer/Horse predominance | Lacarrière, 2018; Bodu et al., 2019 |
| Badegoulian (and related*) | Abri Fritsch - Level 6 (NR=2464) | NR=538 / MNIF=16 | NR=1124 / MNIF=25 | Reindeer/Horse predominance | Poulain, 1984 |
| | Abri Fritsch - Level 5d (NR=2045) | NR=134 / MNIF=5 | NR=1370 / MNIF=33 | Reindeer predominance | Poulain, 1984 |
| | Abri Fritsch - Level 4 (NR=1797) | NR=1080 / MNIF=24 | NR=326 / MNIF=9 | Reindeer/Horse predominance | Poulain, 1984 |
| | Abri Fritsch - Level 3a (NR=598) | NR=245 / MNIF=8 | NR=196 / MNIF=7 | Reindeer/Horse predominance | Poulain, 1984 |
| | Mont-Saint-Aubin Oisy (NR=11125) | NR=274 / MNIF=10 | NR=799 / MNIF=9 | Reindeer/Horse predominance | Bignon, 2008 |
| | Le Colombier Chézy-sur-Marne* (NR=606) | NR=32 / MNIF=4 | NR=293 / MNIF=19 | Reindeer predominance | Montoya et al., 2019 |
| Upper Magdalenian | Etiolles - Amas de cheval (NR=555) | NR=187 / MNIF=3 | NR/MNI=0 | Horse predominance | Bignon, 2008 |
| | Etiolles - D71 (NR=501) | NR=5 / MNIF=1 | NR=256 / MNIF=8 | Reindeer predominance | Bignon-Lau, 2018 |
| | Pincevent - Level IV20 (NR=4643) | NR=37 / MNIF=2 | NR=4542 / MNIF=76 | Reindeer predominance | David et al., 2014; Bignon-Lau, 2014 |
| | Pincevent - Level IV0 (NR=21605) | NR=890 / NNI=34 | NR=1663 / MNI=46 | Reindeer/Horse predominance | Bignon-Lau, 2019 |
| | Tureau des Gardes - TDG10 (NR=4939) | NR=4198 / MNI=89 | NR=733 / MNI=18 | Horse predominance | Bemilli, 1998; Bignon, 2008 |
| | Tureau des Gardes - TDG6 (NR=955) | NR=704 / MNI=10 | NR=201 / MNI=8 | Reindeer/Horse predominance | Bignon, 2008 |
| | Le Grand Canton - Secteur 2 (NR=5494) | NR=5255 / MNI=117 | NR=209 / MNI=14 | Horse predominance | Bridault and Bemilli, 1999; Bignon, 2008 |
| | Ville Saint Jacques (NR=1415) | NR=301 / MNIF=6 | NR=530 / MNIF=19 | Reindeer/Horse predominance | Bignon, 2007b and 2008 |
| | Le Buisson Campin Verberie (NR=17264) | NR=44 / MNIF=6 | NISP=16525 / MNI=130 | Reindeer predominance | Enloe, 2010 |

Table 2 – Faunal spectrum predominance at Last Glacial Maximum and Late Glacial sites in the Paris Basin (NR: Number of Remains, MNI: Minimum Number of Individuals).

Tableau 2 – Prédominances dans les spectres fauniques du Dernier Maximum Glaciaire et du Tardiglaciaire dans les sites du Bassin parisien étudiés. Les descriptions utilisent le Nombre de Restes (NR), le Nombre Minimum d'Individus (NMI).

Tabelle 2 – Vorherrschendes Faunenspektrum in den Fundstellen des Letzten Glazialen Maximums und dem Spätglazial im Pariser Becken (NR: Anzahl der Überreste, MNI: Minimale Anzahl an Individuen).

the Rochefort cave (*Pinus* sp., *Salix* sp., *Juniperus* sp., *Betula* sp.) and offered up five dating results from 20,090 +/- 100 BP to 15,450 +/- 60 BP (Marcoux in Hinguant and Colleter, forthcoming). Furthermore, charcoal from *Betula* sp., dated to 19,150 +/- 50 BP (Erl 17854) was identified within the open air site of Ormesson (Théry-Parisot in Bodu et al., 2014; Bodu et al., 2019). Three other recently dated items confirm the attribution of the site to the Middle Solutrean (two on bones and the third on charcoal; Bodu et al., 2019).

On the Eurasian scale, plant communities were dominated by many species of herbaceous monocots (*Carex* sp., *Juncus* sp.) and dicots (*Artemisia* sp.), and even mosses, as evidenced by pollen and macro remains in the intestines of mummified mammoths (Goetcheus and Birks, 2001; Petit et al., 2008; Van Geel et al., 2008; Normand et al., 2011). A mosaic structure emerges in which steppe-tundra vegetation is associated with loessic areas, and bush tundras developed alongside mesic habitats (Goetcheus and Birks, 2001).

The Expansion-Contraction and the Cryptic Northern Refugia models - opposing or complementary frameworks?

The Expansion-Contraction ('E-C') model of the Pleistocene (Provan and Bennett, 2008) seems to be particularly compatible with the extreme macro-climate conditions described above. This model predicts that depending on expansion-contraction phenomena of glaciers, the large northernmost areas of northern Europe were inhospitable during the most extreme phases. Historically, the palynological syntheses for Europe, performed by Brian Huntley and Harry John Betteley Birks (1983), had largely promoted this model, suggesting a polar desert in the northern regions before the Bølling (Antoine et al., 2003). The 'E-C' model has also been accepted for animal communities (Delpech, 1989 and 1992): according to it, large mammals massively retreated during the worse glacial periods, behind a line stretching from the Loire to the Jura Mountains, due to the extreme lack of available food resources. During these extreme glacial phases, ecological communities retreated further south, towards southern France, or even further to southern peninsulas: Iberia, Italy, and the Balkans. This model, however, does not quite apply to reindeer (*Rangifer tarandus*), because their presence has yet to be attested in Italy during the Upper Palaeolithic. They seem to have remained in Iberia during the Allerød (Álvares-Lao and García, 2010; Álvares-Lao and García, 2011).

Nevertheless, the 'E-C' model, largely based on ancient palynological data, which, moreover, are sensitive to taphonomic alterations, is now in contradiction with the recent archaeo-botanical advances explained earlier. In terms of large mammals, the massive and homogeneous retreat of animal communities no longer holds true, if we are to consider the permanence of hunted animals in the Paris Basin discussed above. This is even clearer for equine populations, because, to stay alive, these animals require large

quantities of food due to their cecum digestive system, which is much less efficient than that of ruminants (Janis, 1976; Duncan, 1992). Furthermore, over the past fifteen years, a number of archaeological discoveries as well as archeobotanical and archeozoological analyses call into question the systematic nature of the 'E-C' model.

Parallel to this, a model arguing for the existence of Cryptic Northern Refugia (CNR) in Europe has emerged, steadily enriched by newly available data.

These cryptic refugia seem to have developed in areas with more favourable micro-climatic conditions and/or sheltered topographies – generally deeply incised valleys in limestone massifs (Stewart and Lister, 2001), throughout the vast ice-free expanses of northern Europe (Binney et al., 2009; Willerslev et al., 2014). But the 'E-C' and the 'CNR' models are not mutually exclusive; they may very well have coincided at certain periods in various regions (fig. 2; Stewart and Lister, 2001; Bennett and Provan, 2008; Provan and Bennett, 2008). Indeed, the 'CNR' might very well have been established during the LGM or during the H2 Heinrich event, concomitantly to certain bio-geographic movements, depending on the various strategies of species and populations. Further investigations (diet, migration, phylogeography) need to be carried out to better understand the evolution and eventual stabilization of populations or communities of 'CNRs' until the beginning of the LG (of the H1 Heinrich event and the Younger Dryas palynological chronozone).

THE STRUCTURING OF ANIMAL COMMUNITIES: PALAEOECOLOGICAL IMPLICATIONS

Expected characteristics of the 'Mammoth Steppe'

The concept of the 'Mammoth Steppe' was notably elaborated by R. D. Guthrie (1982, 1984 and 1990). Here, we will limit ourselves to explaining its three main characteristics. First, the Mammoth Steppe has been recognized as a vast biome (or macro-ecosystem) that developed across most of the Eurasian continent. Chronologically, archaeological data signal its existence for at least all of the Upper Palaeolithic, and until the Holocene in the most northern regions (Hopkins et al., 1982; Zimov et al., 1995; McPhee et al., 2002). This biome is defined by highly diversified plant and animal communities, the result of a long, shared evolutionary history. Taken individually, these specific assemblages appear to be a complex combination of different current biomes, notably the tundra and the steppe (Chernov, 1985). The ecological settlement of the Mammoth Steppe is thus resolutely original and has no clear equivalent today (Guthrie, 1982, 1984 and 1990).

The second characteristic of the Mammoth Steppe is its ecological functioning, intimately linked to its high biodiversity. Today, only a few settlements in African savannas shelter a similarly high diversity of plant and

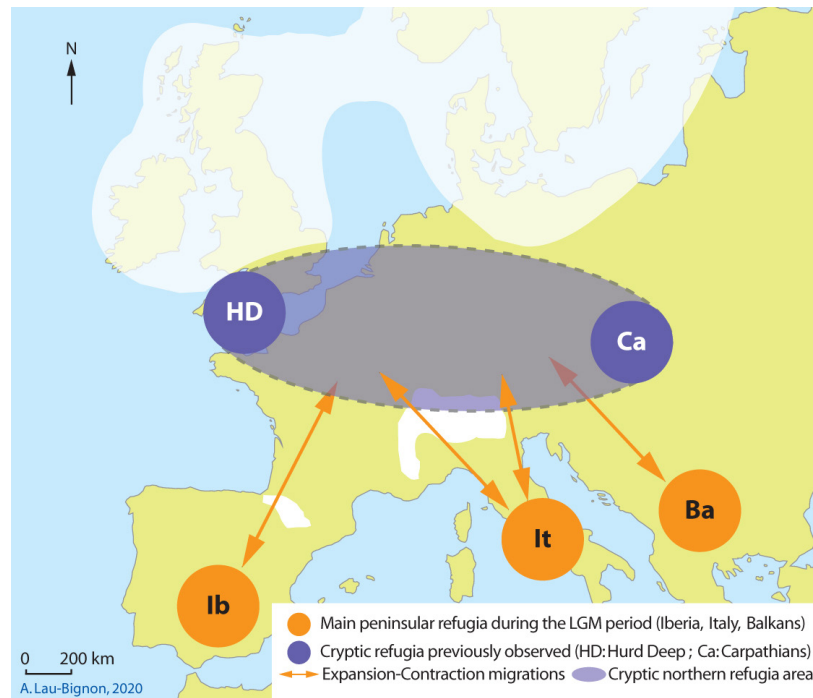


Fig. 2 – Last Glacial Maximum refugia in Western Europe: Cryptic Northern Refugia vs. Southern peninsular refugia areas and Expansion-Contraction ways of migrations (after Stewart and Lister, 2001; Provan and Bennett, 2008, modified).

Fig. 2 – Le Dernier Maximum Glaciaire en Europe occidentale : refuges cryptiques septentrionaux vs refuges des péninsules méridionales et les E-C axes de migrations (d'après Stewart et Lister, 2001 ; Provan et Bennett, 2008, modifiés).

Abb. 2 – Refugien des Letzten Glazialen Maximums in Westeuropa: kryptische nördliche Refugien vs. Refugien der südlichen Halbinseln und Extension-Kontraktion-Migrationswege (nach Stewart und Lister, 2001; Provan und Bennett, 2008, verändert).

animal communities: the common point of all the current communities is the fact that they enjoy open spaces with relatively complex landscape structures. These environments all have grazing ecosystems in which there exist solid and ancient interactions between animal and plant species, as is the case for the Serengeti (Bell, 1970 and 1971; McNaughton, 1984 and 1994). This is necessarily an analogous comparison because specific components from the Palaeolithic do not correspond to those in the Serengeti. However, in both cases, the complementarity of animal diet, their migrations, and interactions can only be explained by the existence of grazing ecosystems and open, diverse landscapes.

The third characteristic of the Mammoth Steppe deals directly with the mosaic structure of landscapes at the regional level. This complex arrangement reflects the mosaic composition of all the animal and plant species (Guthrie, 1982 and 1984). Though it is possible today to observe a latitudinal leveling of biomes from the North Pole to the equator, R. D. Guthrie (ibid.) developed a biogeographical 'patchwork quilt' model for the Palaeolithic periods. This model allows for an understanding of the mosaic structure of landscapes (linked to the characteristics of the physical environment) at regional and continental levels.

Such non-analogue animal assemblages have been investigated using isotopic analysis of collagen in order to verify the characteristics of the Mammoth Steppe. A large survey of southwest France throughout the Upper Palaeo-

lithic (Drucker, 2001) is highly consistent with Guthrie's model. The results showed an open environment without dense tree cover in which the various herbivores shared food resources following specific trends through time.

Faunal spectrum and the structure of animal communities during the LGM and the LG in the Paris Basin

Compiled in a recent article (Bignon-Lau et al., 2019), at least 150 radiocarbon datings on bones from large mammals were confirmed for the LMG period and the H2 Heinrich event in the northernmost zones of western and central Europe. These dates, which correspond to what is probably still an incomplete survey of data, confirm the presence of large animal communities in these geographic areas (tables 1 and 3).

What is remarkable is the relative importance of megaherbivore species (Owen-Smith, 1988) with one fifth of the radiocarbon datings. This category of monogastric herbivores (with a cecum digestive system) includes species that consume large quantities of plant matter. In order of importance, there were woolly mammoths (*Mammuthus primigenius*), horses (*Equus caballus* sp.), and woolly rhinoceroses (*Coelodonta antiquitatis*). These animals theoretically fed off of large quantities of herbaceous plants and grasses, suggesting a relative abundance of plant resources, at least within certain fringes of the landscape (Owen-Smith, ibid.).

| Cultural entities | Sites & levels | Monogastric Herbivores | Ruminant Herbivores | Carnivores | Omnivores |
|-------------------|---|---|---|--|--|
| Solutrean | Abri Fritsch | | | | |
| | Level 10b (NR = 505) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> | <i>Canis lupus</i> <i>Vulpes</i> sp. | |
| | Level 9 (NR = 2479) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> | <i>Canis lupus</i> <i>Mustela putorius</i> | |
| | Level 8b (NR = 5731) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> <i>Cervus elaphus</i> , <i>Capra ibex</i> <i>Saiga tatarica</i> , <i>Bos/Bison</i> | | |
| | Level 7b (NR = 2328) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> <i>Saiga tatarica</i> <i>Bos/Bison</i> | <i>Vulpes vulpes</i> <i>Vulpes</i> sp. | |
| | Les Bossats Ormesson (NR = 230) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> <i>Bos/Bison</i> | | |
| | Grotte Rochefort (NR = 5500) | <i>Mammuthus primigenius</i> <i>Coelodonta antiquitatis</i> <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> <i>Capreolus capreolus</i> <i>Capra ibex</i> <i>Bos/Bison</i> | <i>Canis lupus</i> <i>Vulpes vulpes</i> <i>Vulpes lagopus</i> <i>Lynx</i> sp., <i>Felix sylvestris</i> <i>Ursus arctos</i> | <i>Sus scrofa</i> |
| Badegoulian | Abri Fritsch | | | | |
| | Level 6 (NR = 2464) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> <i>Capra ibex</i> <i>Bos/Bison</i> | <i>Canis lupus</i> <i>Meles meles</i> <i>Vulpes</i> sp. | <i>Sus scrofa</i> <i>Ursus spelaeus</i> |
| | Level 5d (NR = 2045) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> <i>Capra ibex</i> <i>Bos/Bison</i> | <i>Canis lupus</i> <i>Mustela nivalis</i> <i>Vulpes</i> sp. | <i>Sus scrofa</i> <i>Ursus spelaeus</i> |
| | Level 4 (NR = 1797) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> <i>Capra ibex</i> <i>Bos/Bison</i> | <i>Mustela putorius</i> <i>Vulpes</i> sp. | <i>Ursus spelaeus</i> |
| | Level 3a (NR = 598) | <i>Equus caballus</i> sp. | | <i>Canis lupus</i> <i>Mustela nivalis</i> <i>Vulpes</i> sp. | <i>Ursus spelaeus</i> |
| | Mont-St-Aubin - Oisy (NR = 11125) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> <i>Bison priscus</i> | <i>Canis lupus</i> <i>Ursus arctos</i> | |
| | Le Colombier Chézy-sur-Marne (NR = 606) | <i>Equus caballus</i> sp. | <i>Rangifer tarandus</i> | | |

Table 3 – Last Glacial Maximum faunal communities' structuration at Paris Basin sites.

Tableau 3 – Structuration des communautés animales du Dernier Maximum Glaciaire d'après les sites étudiés du Bassin parisien.

Tabelle 3 – Strukturierung der Faunengemeinschaften während des Letzten Glazialen Maximums in den Fundstellen des Pariser Beckens.

However, ruminants are represented by the vast majority of the datings. These animals, which are more selective in their choice of plants or parts of plants, generally placed less of a strain on the plant resources in their environment due to their more efficient digestive system (Janis, 1976; McNaughton, 1984 and 1994). In this category, the reindeer (*Rangifer tarandus*) is by far the best documented species, though the red deer (*Cervus elaphus*) is also well represented in central France and central Europe. Other ruminants included the Irish elk (*Megaloceros giganteus*) and even the roe deer (*Capreolus capreolus*). Though they have been found at certain sites, large bovines (aurochs, bison) suffer from an incomprehensible lack of dating.

For carnivores, the majority of available datings concern hyenas (*Crocota* sp.), more rarely are there wolves (*Canis lupus*), or other mid or small species, such as the polar or common fox (*Vulpes lagopus*, *Vulpes vulpes*), or the wolverine (*Gulo gulo*), but also the arctic lemming as a rodent (*Dicrostonyx torquatus*).

As is the case with plant communities, the direct datings of animal remains, though less abundant in current research, confirm the presence of diversified communities

in northern Europe during the LGM. Moreover, in the Paris Basin, there is little difference in animal communities between the LGM and the LG (table 2). However, this similarity in the structuring does not mean that they had the same palaeoecological functions as shown by current studies on large animal communities (Sinclair et al., 2003; Fryxell et al., 2005; Hopcraft et al., 2010). Indeed, Mammoth Steppe communities with identical or near identical compositions can have fairly different modes of ecological functioning (in terms of demographic balance, physical environment, or hydrographic networks; see Bignon, 2008 and 2009; Bignon-Lau et al., 2019). If we take into consideration the climate conditions and characteristics of the Mammoth Steppe, we should arrive at an ecological structuring of communities in the northern regions of France that was even more diversified during the LGM. This organisation would imply a variable, regional abundance of taxa and thus a specific density that fluctuates locally or over time. Providing an annual diet summary, the isotopic analysis of collagen realized on herbivores found at the Paris Basin sites revealed a tundra-like environment, but this area has not been as well investigated

as southwestern France (Drucker, 2007a, b and 2011a, b). However, many horses ($n = 28$) and reindeer ($n = 21$) from Magdalenian and Early Azilian sites have been analysed: Etiolles (Locus 2), Verberie, Pincevent (IV0, IV20, IV.21.3, Habitation 1), and Le Closeau. Reindeer values ($\delta^{13}\text{C}_{\text{coll}} = -19.3$ and -20.3 ‰; $\delta^{15}\text{N}_{\text{coll}} = 1.6$ and 3.9 ‰) clearly indicate the consumption of lichens and a certain variability of environmental contexts, where resources were found by these ruminants. Horse values ($\delta^{13}\text{C}_{\text{coll}} = -20.3$ and -21.8 ‰; $\delta^{15}\text{N}_{\text{coll}} = 1.8$ and 5.4 ‰) exhibit more steppic features (without lichens in their diet), while the great variability in nitrogen observed reveals a wide set of environmental conditions (namely, a more or less pronounced aridity or a fertilization of soils). Such results, even if restricted to the LG and limited specimens per site, clearly show that reindeer and horse frequented an open environment and avoided direct food competition.

To address the resource partitioning in the Paris Basin during the LGM and LG with larger samples, keeping in mind the ecological structure of animal communities, we tracked the feeding habits of the reindeer and horses using dental microwear textural analyses. This approach allowed us to also examine the stability of coevolutionary ties that linked these prey with their human predators.

FEEDING HABITS OF KEY PREYS

A multiscale approach

The presence of horses and reindeer has been attested at most of the Upper Palaeolithic sites in the Paris Basin, when fauna was preserved (table 3). By reconstructing the feeding habits of these two taxa, both at the inter- and intra-specific levels, we have arrived at hypotheses on the environment they inhabited (composition, structuring, and functioning of animal communities), and on the utilization of animal resources by human societies. To optimise the perception of the results, we opted for a multiscale approach, much more commonly used in biogeography (Blondel, 1995), in order to discriminate between the different sources of variability in feeding habits:

- At the inter-individual level, variability is considered at the local level and within the same, specific population, in other words, at the scale of the archaeological site (LGM or LG);

- At the inter-population level, the regional level of the Paris Basin during the chronological phases (LGM, LG) is the framework for differentiating variables. Though it is possible within current dataset frameworks to potentially consider the variations between populations within or between two sub-species of a taxa, this degree of resolution is not possible for Palaeolithic taxa. We are obliged to use the less well-defined ‘chrono-species’ that are most often established using morphotypes (with osteometry or morphometry).

- At the inter-specific level, in our case between reindeer and horses, observations were made at the regional/continental level, following the main chronological

phases under consideration, in order to study both the evolutionary tendencies and the interaction between each species-specific behaviours. This scale further requires large sets of actualist and archaeological data, with vastly improved equine datasets. Our first observations are thus illustrative and not definitive. How to reconstitute the diet of the herbivores studied here?

Method

When plants are chewed by animals, they scratch tooth enamel and leave microscopic wear. This microwear can be characterised to reconstitute an individual’s diet during the final weeks of its life (Merceron et al. 2004 and 2016; Scott, 2012). The protocol for dental microwear texture analysis (DMTA) is applicable across all species (Calandra and Merceron, 2016; Scott et al., 2005, 2006 and 2009; Ungar et al., 2008a, b and 2010; Krueger and Ungar, 2009; Martin et al. 2018; Merceron et al., 2009 and 2016; Prideaux et al., 2009; Ungar and Scott, 2009; Schubert et al., 2010; Schulz et al., 2010). Following standard procedures, teeth were selected, cleaned, and dental molds were made using President microSystem Affinis Regular body (Coltène-Whaledent) polyvinylsiloxane. The replicas were then scanned using the ‘TRIDENT’ white light confocal surface profilometer DCM8 Leica Microsystems (at the PALEVOPRIM laboratory, CNRS, and the University of Poitiers), which was used to produce a 3D model of dental surfaces. Finally, the last step in obtaining data was an automatic calculation using multi-scalar analyses of textural parameters (Scott et al., 2006). Then, Toothfrax and Mountain software were used to generate DMTA variables, following procedures and settings provided by Scott et al. (2006).

To date, three parameters synthesize information on dietary habits: anisotropy (epLsar [= exact proportion of Length-scale anisotropy of the relief]), complexity (Asfc [= Area-scale fractal complexity]), and the heterogeneity of complexity (HASfc [= heterogeneity of Area-scale fractal complexity]). Food ingested by ruminants is differentiated by its nutritional and physical properties. Abrasives (both endogenous phytoliths and, to a lesser extent, exogenous dust; Merceron et al., 2016) within tissues and the mechanical and physical properties of fodder scratch the surface of the enamel. The more these scratches are preferentially oriented (high anisotropy epLsar), the more likely it is that the animal is a tough-leaf eater. It is more specifically a grazer (Scott, 2012), if the anisotropy is coupled with a low or very low complexity values. Grazers show lower complexity (Asfc) and higher anisotropy (epLsar) values than intermediate feeders and browsers (Ungar et al., 2007; Scott, 2012). Among browsers, those that ingest few lignified tissues tend to have lower complexity values than species with diets including bark, seeds, and twigs. Browsers may also have high anisotropy values (coupled with intermediate complexity), if the dietary bolus is composed of tough leafy material (Merceron et al. 2021, in press). Grazers would have ingested large quantities of plants rich in phytoliths such as herbaceous monocots

(grasses, sedges, rushes). The more mature the monocotyledons, the higher the concentration of phytoliths. Finally, heterogeneity of complexity (HASfc) values are low with a poorly diversified diet and, in opposition, this parameter's values rise when diets diversify (Souron et al., 2015; Ramdarshan et al., 2016; Calandra and Merceron, 2016; Merceron et al., 2018).

The study of dental microwear allows us to reconstitute the variability of dietary habits, for example throughout a season (Merceron et al., 2010; Percher et al., 2018; Berlioz et al., 2017). Among ruminants, there are three types of dietary habits:

- Grazers that eat herbaceous monocotyledons, including sedges, rushes, and grasses. These plants share a higher concentration of silica phytoliths than most dicotyledon plants (physical defenses of plants; Hodson et al., 2005; Massey et al., 2007) and mark the dental enamel of ruminants.

- Browsers are more diversified than grazers. They include different tissues or parts of trees (stems, leaves, shrubs, flowers, fruit) in their diet. The physical defenses of plants thus vary depending on the tissues ingested.

- Mixed feeders are more or less grazers or browsers depending on the availability of resources in the landscape.

It is thus possible to identify the different feeding habits of herbivores according to the selection of plants ingested. By identifying such a selection, we obtain a clearer image of these animals' habitats, because the distribution and diversity of plants respond to certain environmental characteristics. We thus have indications on the areas where prey may have been killed by hunters.

Material

We studied reindeer from two LGM sites and horses from three LGM sites (table 4). We were able to compare diet data for reindeer from four LG sites and for horses with data from one LG site. The majority of these sites offers samples of the two species most hunted by humans during the Upper Palaeolithic. For certain deposits (Pincevent level IV0, Rochefort), we conducted analyses on both species, which allowed us to compare the behaviour of reindeer and horses in the same occupation area (intra-species/inter-site or inter-species/intra-site scales). For the other sites, data was either not available or available but analysed for only one of the two species studied here.

The archaeological findings were then compared with the dental datasets of modern African bovids covering the whole spectrum from browsers to grazers (Scott, 2012). We also used modern dental datasets from the few horses available housed in the Zoological Museum of Copenhagen alongside two datasets from Norwegian reindeer – the first one is being established and the second one has already been published (table 4; Bignon-Lau et al., 2017). Here below, we present the first findings on three types of reindeer populations. The study of continental, alpine tundra reindeer (n = 123; Bignon-Lau et al., 2017) from the Hardangervidda and Knutshø regions in southern Norway helped shape our hypothesis on the adjustment of

diets in terms of the availability of resources in the environment and the density of the population within a single region. The study of reindeer from three valleys of the Svalbard archipelago (Colesdalen: n = 420, Sassendalen: n = 503, Grøndalen: n = 79) and of a reindeer population from the forests of a continental region (Forollhogna: n = 55) helped refine our observations on the plasticity of reindeer diets.

For our study on reindeer and horses, we selected only teeth that presented optimal enamel surface conservation. Faunal remains were better preserved from one site/level to another (Pincevent: level IV0 versus level IV20, for instance; Bignon-Lau, 2019); but in accordance with our selection criteria, such taphonomic differences did not affect the specimens analysed. For reindeer, DMTA was performed on disto-labial facets on the protoconid of lower molars. Priority was given to M2, and additional analyses were carried out on homologous dental facets on third or first molars, following the recommendations of Ramdarshan et al. (2016). For horses, any tooth (upper, lower, premolar, molar) was selected, since no significant differences appeared when using lingual or vestibular enamel facets from one tooth to another (Schulz et al., 2010).

Dietary habits in extant reindeer and Palaeolithic reindeer

As all other ruminants, the reindeer is selective and therefore categorized as an intermediate feeder/browser (Danell et al., 2006). Studies on modern *Rangifer tarandus* show they eat lichen (*Cladonia rangiferina* L.) all year round (Skogland, 1980). However, the plasticity of their dietary habits depends directly on their environment's resources. This plasticity has been proven through analyses of their stomach contents (Kuntz, 2011), because other foods are consumed throughout the seasons: mushrooms, dicot and monocot plants (grasses, rushes, sedges), moss, and sometimes even leaves from shrubs and trees (alder, birch, willow). Finally, they also occasionally eat small mammals and bird's eggs (Leader-Williams, 1988 – as cited in Kuntz, 2011).

Dental microwear texture analyses carried out on modern day reindeer in Norway (fig. 3; table 4) illustrate the plasticity of diets within the same species in various environments:

- Continental, alpine tundra reindeer (*Rangifer t. tarandus*), slaughtered at the end of summer at Hardangervidda and Knutshø, are mixed feeders.

- Continental, alpine tundra reindeer (*Rangifer t. tarandus*), slaughtered during winter in Hardangervidda, more closely resemble browsers.

- Tundra alpine reindeer from Spitsbergen (Svalbard; *Rangifer t. platyrhynchus*) – all populations slaughtered between August and September – are obligate grazers.

- Reindeer from Forollhogna (*Rangifer t. tarandus*), slaughtered between August and September, behave like forest reindeer with dental wear more closely resembling that of browsers.

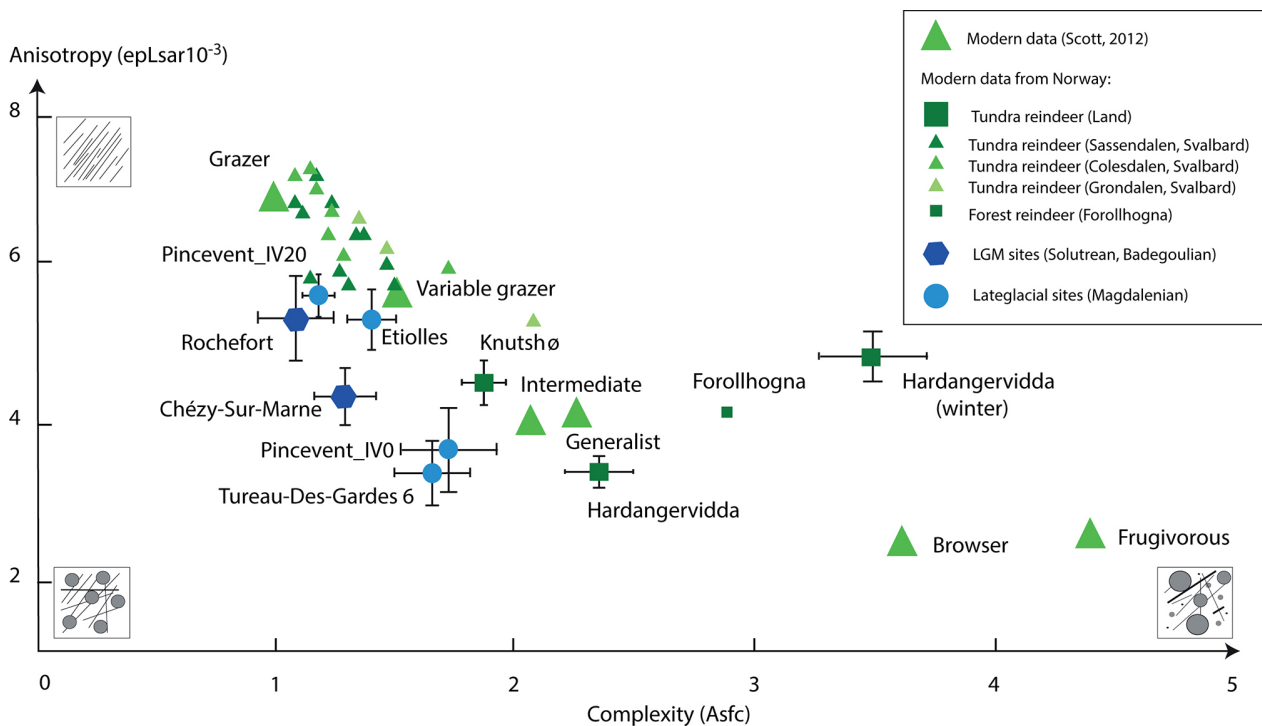


Fig. 3 – Reindeer dental microwear textures and diets from the study using complexity (Area-scale fractal complexity, Asfc) and anisotropy (exact proportion Length-scale anisotropy of the relief, epLsar). Standard error of the mean indicated for archaeological and main continental actual populations.

Fig. 3 – Analyses texturales des micro-usures dentaires de renne de cette étude et les régimes alimentaires, utilisant les paramètres de Complexité (Area-scale fractal complexity, Asfc) et d'Anisotropie (exact proportion Length-scale anisotropy of the relief, epLsar). Les écarts-types à la moyenne sont indiqués pour les populations archéologiques et actuelles continentales.

Abb. 3 – Mikrospuren-Textur an Rentierzähnen und Ernährungsweise aufgrund von Komplexität (fraktale Komplexität im Flächenmaßstab, Asfc) und Anisotropie (genaues Verhältnis Anisotropie des Reliefs im Längenmaßstab, epLsar). Standardfehler des angegebenen Mittelwerts für archäologische und tatsächliche kontinentale Populationen.

Compared to these reindeer, Palaeolithic reindeer of the LGM and the LG offer lower complexity values (Asfc), whether they were grazers or browsers. Because of this, prehistoric reindeer plot just below modern ones (fig. 3), suggesting an evolution in resource consumption.

According to dental microwear texture analyses, the LGM reindeer at Rochefort cave and Chézy-sur-Marne offer very high anisotropy and very low complexity values (fig. 3). While these sites do show a relative variability, this cannot be interpreted as a result of distinct behaviours during this period. Though variability between individuals appears more pronounced in Rochefort, there is no overlapping of specimens between both sites.

During the LG, once again, we can observe a diversity of feeding habits in reindeer (fig. 3). Grazing can be observed in both cases of the IV20 level of Pincevent and Étiolles (Locus 2) specimens, which present high anisotropy (epLsar) and low complexity (Asfc) values. These findings contrast with those of the reindeer of level IV0 of Pincevent and of Tureau des Gardes, aligning more with mixed feeder herbivores (lower anisotropy and higher complexity). It should be noted that, at level IV20 of Pincevent and Étiolles, the inter-individual variability of specimens is low, sufficiently for there to have been no inter-population overlap of specimens between

the two sites. In contrast, the reindeer of Pincevent level IV0 and those of Tureau des Gardes 6 display a relatively higher intra-population variability, compared to the two previously mentioned sites/levels, and show a large inter-population overlap. At Pincevent level IV0 and Tureau-des-Gardes 6, seasonal estimations offer information on the killing of individual specimens throughout the year (Bignon et al., 2006; Bignon, 2008; Debout et al., 2012): the high inter-individual dispersion thus corresponds to the maximum amplitude of annual values. To conclude, specimens of the level IV20 of Pincevent and Étiolles exhibit grazing behaviour and a very low inter-population variability, while specimens of the level IV0 of Pincevent and Tureau des Gardes 6 show mixed feeder habits and a larger variability corresponding to a year-round values. Simply put, when values are available for only a season, variability is necessarily reduced. Considering the annual intra-population variability of actual Hardangervidda specimens, such an interpretation for the two latest LG sites looks very likely consistent.

Finally, the inter-population levels (range of dietary habits) seem greater during the LG than during the LGM, between the reindeer of Pincevent IV20/Étiolles on the one hand and those from Pincevent IV0/Tureau des Gardes 6 on the other.

| Sites | Year/Period | Species | n | Asfc | | | epLsar10 ⁻³ | | |
|-----------------------|--------------------|----------|----|-------|-------|-------|------------------------|-------|-------|
| | | | | mean | s.d. | s.e.m | mean | s.d. | s.e.m |
| CSM | <i>Badegoulian</i> | Rangifer | 21 | 1.286 | 0.590 | 0.129 | 4.185 | 1.550 | 0.338 |
| Etiolles | <i>Magdalenian</i> | Rangifer | 20 | 1.392 | 0.453 | 0.101 | 5.151 | 1.635 | 0.366 |
| Pinc_IV0 | <i>Magdalenian</i> | Rangifer | 13 | 1.716 | 0.724 | 0.201 | 3.520 | 1.858 | 0.515 |
| Pinc_IV20 | <i>Magdalenian</i> | Rangifer | 55 | 1.169 | 0.489 | 0.066 | 5.453 | 1.876 | 0.253 |
| Pinc_IV21 | <i>Magdalenian</i> | Rangifer | 2 | 2.337 | 0.023 | 0.016 | 2.720 | 1.663 | 1.176 |
| TDG6 | <i>Magdalenian</i> | Rangifer | 12 | 1.650 | 0.552 | 0.159 | 3.234 | 1.382 | 0.399 |
| Rochefort | <i>Solutrean</i> | Rangifer | 25 | 1.079 | 0.499 | 0.100 | 5.175 | 2.557 | 0.511 |
| Hardangervidda | Winter | Rangifer | 21 | 3.539 | 0.892 | 0.195 | 4.727 | 1.043 | 0.228 |
| Hardangervidda | 2014 | Rangifer | 54 | 2.344 | 1.043 | 0.142 | 3.254 | 1.393 | 0.190 |
| Knutshø | 2014 | Rangifer | 48 | 1.865 | 0.640 | 0.092 | 4.36 | 1.867 | 0.269 |
| Forollhogna | 2017 | Rangifer | 55 | 2.874 | 0.956 | 0.129 | 4.211 | 1.630 | 0.220 |
| Colesdalen | 1984 | Rangifer | 33 | 1.719 | 0.996 | 0.173 | 5.836 | 2.226 | 0.388 |
| Colesdalen | 1995 | Rangifer | 13 | 1.143 | 0.539 | 0.150 | 7.084 | 2.157 | 0.598 |
| Colesdalen | 1996 | Rangifer | 30 | 1.219 | 0.608 | 0.111 | 6.268 | 1.991 | 0.364 |
| Colesdalen | 1997 | Rangifer | 23 | 1.071 | 0.452 | 0.094 | 6.992 | 2.055 | 0.428 |
| Colesdalen | 1998 | Rangifer | 19 | 1.167 | 0.483 | 0.111 | 6.867 | 2.321 | 0.532 |
| Colesdalen | 2006 | Rangifer | 28 | 1.237 | 0.689 | 0.130 | 6.561 | 2.370 | 0.448 |
| Colesdalen | 2007 | Rangifer | 21 | 1.287 | 0.516 | 0.113 | 5.996 | 2.364 | 0.516 |
| Grondalen | 1984 | Rangifer | 30 | 1.334 | 0.441 | 0.080 | 6.240 | 2.406 | 0.439 |
| Grondalen | 1986 | Rangifer | 10 | 2.069 | 1.158 | 0.366 | 5.176 | 1.198 | 0.379 |
| Grondalen | 1987 | Rangifer | 10 | 1.454 | 0.448 | 0.142 | 6.097 | 2.301 | 0.728 |
| Grondalen | 1995 | Rangifer | 17 | 1.345 | 0.388 | 0.094 | 6.454 | 1.690 | 0.410 |
| Sassendalen | 1984 | Rangifer | 20 | 1.294 | 0.471 | 0.105 | 5.635 | 1.942 | 0.434 |
| Sassendalen | 1986 | Rangifer | 28 | 1.254 | 0.485 | 0.092 | 5.820 | 2.166 | 0.409 |
| Sassendalen | 1987 | Rangifer | 20 | 1.108 | 0.375 | 0.084 | 6.536 | 2.379 | 0.532 |
| Sassendalen | 1995 | Rangifer | 22 | 1.482 | 0.720 | 0.153 | 5.645 | 2.037 | 0.434 |
| Sassendalen | 1996 | Rangifer | 17 | 1.169 | 0.491 | 0.119 | 7.012 | 1.343 | 0.326 |
| Sassendalen | 1997 | Rangifer | 44 | 1.229 | 0.570 | 0.086 | 6.673 | 1.722 | 0.260 |
| Sassendalen | 1998 | Rangifer | 35 | 1.460 | 0.815 | 0.138 | 5.877 | 2.233 | 0.378 |
| Sassendalen | 2006 | Rangifer | 49 | 1.079 | 0.496 | 0.071 | 6.655 | 2.153 | 0.308 |
| Sassendalen | 2007 | Rangifer | 20 | 1.355 | 0.823 | 0.184 | 6.257 | 2.420 | 0.541 |
| Sassendalen | 2014 | Rangifer | 27 | 1.141 | 0.595 | 0.115 | 5.698 | 2.869 | 0.552 |
| Greenland | - | Equus | 1 | 2.754 | - | - | 4.074 | - | - |
| Przewalski | - | Equus | 2 | 3.086 | 2.013 | 1.423 | 2.708 | 2.070 | 1.464 |
| Exmoor | - | Equus | 1 | 3.866 | - | - | 0.798 | - | - |
| Iceland | - | Equus | 9 | 3.864 | 2.208 | 0.736 | 1.772 | 1.794 | 0.598 |
| Rochefort | <i>Solutrean</i> | Equus | 41 | 1.186 | 0.707 | 0.110 | 3.776 | 2.013 | 0.314 |
| Abri Fritsch | <i>Badegoulien</i> | Equus | 12 | 1.940 | 0.857 | 0.247 | 5.395 | 1.764 | 0.509 |
| Renancourt | <i>Gravettian</i> | Equus | 15 | 1.518 | 0.487 | 0.126 | 3.959 | 2.993 | 0.773 |
| Pincevent IV0 | <i>Magdalenian</i> | Equus | 16 | 2.509 | 1.226 | 0.307 | 2.991 | 1.673 | 0.418 |

Table 4 – Archaeological and modern reindeer and horse specimens used in dental microwear textural analyses.

Tableau 4 – Spécimens de renne et de cheval archéologiques et modernes utilisés dans nos analyses texturales de micro-usures dentaires.

Tabelle 4 – Archäologische und moderne Rentier- und Pferde-Proben, die zur Analyse der dentalen Mikrosuren genutzt wurden.

Dietary habits of modern day horses and their Palaeolithic counterparts

According to contemporary knowledge, a horse is depicted as a generalist herbivore, though it systematically consumes a wide range of plants and among them a large amount of grasses (Duncan, 1992; Bignon, 2008). The equine cecum digestive system specifically encourages these animals to choose plants with physical defenses (grasses, rushes, reeds, etc.) rather than those with chemical defenses. As a result, due to this generally more abrasive diet, horses are much more dependent on sources of water than reindeer (Skogland, 1989; Duncan, 1992).

Data on recent horses obtained from the Zoological Museum of Copenhagen are much less developed than those for reindeer – we aim to reinforce them significantly in the very near future (table 4). The values for the horses of Exmoor (UK) or Iceland (fig. 4) seem to indicate leafy feed, as illustrated by their typical positioning of browsers. In contrast, we are more confident in the values of the Przewalski horses (hunted in the Gobi desert at the beginning of the 20th century) and those from Greenland that gravitate around the values for generalist herbivores.

Though archaeological data on horses are less abundant in comparison to those on reindeer, both in number of sites and specimens, we do not find systematically

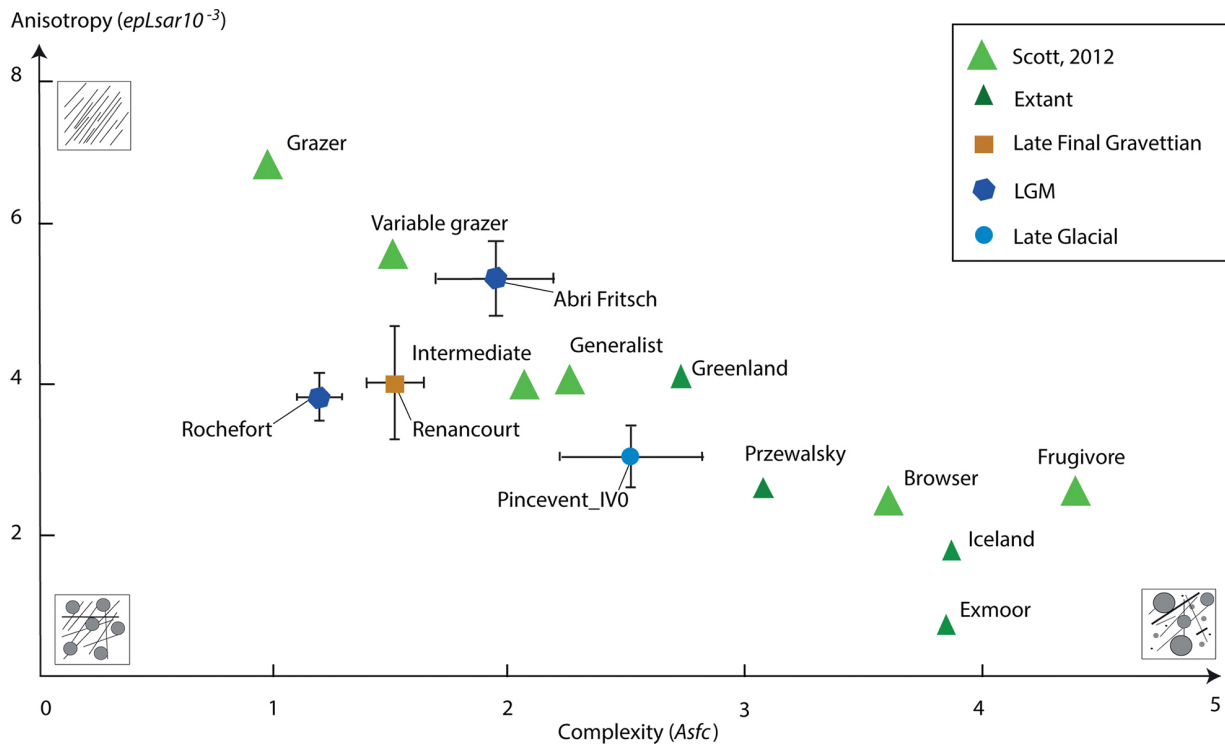


Fig. 4 – Horse dental microwear textures and diets from the study using complexity (Area-scale fractal complexity, Asfc) and anisotropy (exact proportion Length-scale anisotropy of the relief, epLsar). Standard error of the mean indicated for archaeological populations.

Fig. 4 – analyses texturales des micro-usures dentaires de cheval de cette étude et les régimes alimentaires, utilisant les paramètres de Complexité (Area-scale fractal complexity, Asfc) et d'Anisotropie (exact proportion Length-scale anisotropy of the relief, epLsar). Les écarts-types à la moyenne sont indiqués pour les populations archéologiques et actuelles continentales.

Abb. 4 – Mikrospuren-Textur an Pferde Zähnen und Ernährungsweise aufgrund von Komplexität (fraktale Komplexität im Flächenmaßstab, Asfc) und Anisotropie (genaues Verhältnis Anisotropie des Reliefs im Längenmaßstab, epLsar). Standardfehler des angegebenen Mittelwerts für archäologische Populationen.

higher levels of complexity (Asfc) among horses when compared to their modern day counterparts. While the horses of Amiens-Renancourt 1 and the Rochefort cave (the two oldest sites) comply with 'Palaeolithic' tendencies like those observed on reindeer, this is not true for the equines from the Fritsch shelter (Badegoulian levels) and those from level IV0 of Pincevent.

During the LGM, according to dental microwear texture analyses, the horses of the Rochefort cave present an intermediate anisotropy and low level complexity, which allows them to be classified as generalists or intermediate feeders (fig. 4). For example, the horses of Amiens-Renancourt 1, before the LGM (table 1), tend to show a generalist behaviour that is ultimately similar to the equines of the Rochefort cave. At the Fritsch shelter, the horses present a stronger anisotropy than other horses and a higher level of complexity than the reindeer studied. They seem to be variable or intermediate grazers (fig. 4). Another interesting point is that inter-individual variability fluctuates depending on the sites: the horses of the Rochefort cave have more concentrated values (even though data are more abundant; table 4), compared to Amiens-Renancourt 1 (anisotropy) or the Fritsch shelter (complexity).

When comparing the horses of the LG and the LGM, we observed noteworthy differences with horses from Pincevent (niveau IV0; fig. 4). The latter show generalist

herbivore values with a tendency towards browsers (less pronounced than the horses from Iceland or the Przewalski ones), whereas those from the LGM have on the contrary a tendency towards grazing. Finally, the horses at level IV0 of Pincevent offer up the highest level of inter-individual variability of all the archaeological species. This might be tied to the generalist nature of their diet, but it could also be due to the maximal amplitude of annual values, as these horses were hunted all year round (Bignon et al., 2006; Bignon, 2008; Debout et al., 2012). It is clear that recent specimens' datasets as well as complementary studies of other sites from the same period are necessary to consolidate and compare these preliminary results.

CONFRONTING THE RESULTS WITH THEIR ENVIRONMENTAL CONTEXTS

In linking palaeoecological groups of herbivores (monogastrics, ruminants) to representative species (horse, and reindeer, respectively), our research strategy was to track evolution and to describe their feeding habits through the LGM and LG periods. Obviously, this work in progress cannot resolve and explain the whole of palaeoecological complexity at the end of the Pleistocene; however,

combining functional groups with microwear analyses currently offers significant data. In line with rare pioneering studies (Price et al. 2017), we will be comparing our current data with strontium, carbon, and oxygen isotopic analyses of bioapatite (sequential bands of tooth enamel), when completed (Catz, doctoral thesis, ongoing).

Our data thus indicates that the horses and reindeer of these globally cold periods managed, despite the climate conditions, to find plant resources in sufficient quantity, mostly herbaceous monocotyledons (with strong anisotropy tendencies) that were also relatively varied. Based on this diet, the palaeoenvironment would seem to have been an open landscape with plant life similar to our modern steppe plains. Our observations confirm the model of a Mammoth Steppe, even during the LGM, which does not resemble a polar desert. It was, at least in certain areas, ideal pasture land for both ruminants and mono-gastric animals. As previously suggested by the isotopic analysis of collagen realized on herbivore remains from sites throughout the Upper Palaeolithic in southwest France or from the Paris Basin during the LG (Drucker, 2001 and 2007a, b; Drucker et al., 2011a, b), our results indicate a probable partition of plant resources in the latter region since the LGM.

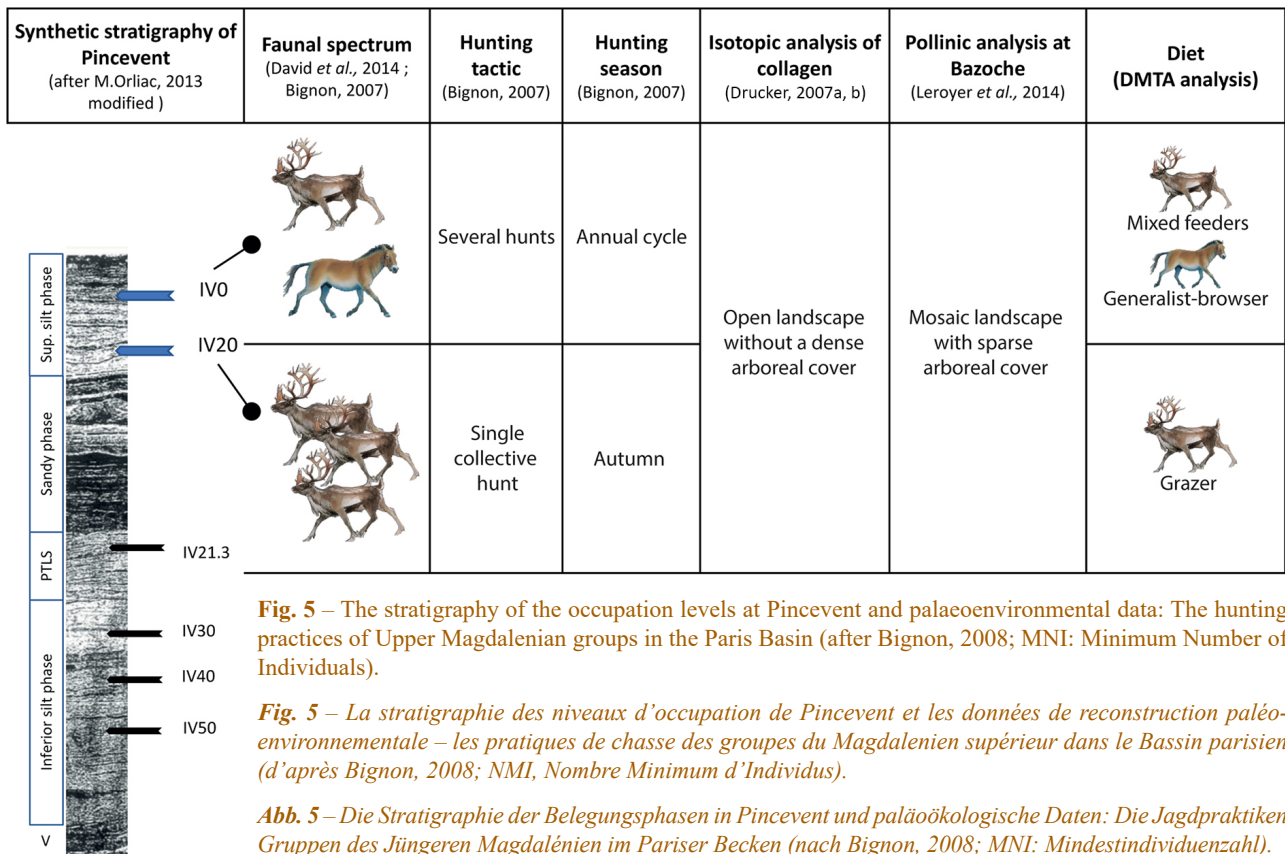
As for reindeer during the LGM and the LG, we observed relatively limited variations in diet between individuals within populations that lived in the same types of habitats. For cervids, the inter-population variations are more contrasted between mixed feeder and grazer diets, both during the LGM and the LG, thus with no linear evolution in time. These inter-population variations were discovered among the alpine tundra reindeer in Norway (Knutshø and Hardangervidda; Bignon-Lau et al., 2017), as well as between these specimens and those in Spitsbergen (fig. 3; Bignon-Lau et al., in preparation). Furthermore, even though ethologist data (Danell et al., 2006) state that modern reindeer have a flexible diet, ranging from intermediate herbivores to browsers, the Palaeolithic reindeer differ from this with generalist herbivore behaviour with strong grazer tendencies. In addition, this tendency was also observed among Hardangervidda reindeer. These cervids were hunted during two distinct seasons: late summer and winter. Observing these data, we thus can underline the variation of complexity in diet from one period to another. This seems to be the result of two distinct behaviours that are dictated by growth patterns in plant resources and a change in diet from summer grass consumption (grazer) to winter lichen consumption (browser). Finally, our datasets on the Spitsbergen reindeer clearly point to grazing behaviours, at least for the period between late August and the beginning of October. Usually, only the crucial role of lichens is mentioned for the LG reindeer diet (Rivals et al., 2020), thus dental microwear texture analyses presented here bring substantial data.

Dental microwear texture analyses of reindeer killed by Magdalenian hunters in Pincevent have revealed rapid variations in feeding behaviour between different levels of occupation (Catz, 2016; Catz et al., 2020; figs. 3, 5). It is possible to observe a link between hunting strategies

with micro-wear data. When reindeer dominated the faunal spectrum at level IV20 (Julien and Karlin, 2014), they behaved like grazers. However, when both reindeer and horses dominated the spectrum at level IV0 (Bignon et al., 2006; Debout et al., 2012), they adopted a more diversified diet similar to intermediate herbivores. The nutritional ecology of prey determines key parameters such as their spatial and seasonal distribution, which in turn influences hunting choices in terms of availability of resources, herd density, etc.; we can thus appreciate the significant impact of animal feeding habits on hunting strategies. Considering the grazing habits of both horses and reindeer, the graminoid fields in which they foraged may have provided good cover for hunters engaged in stalking or other hunting approaches in such open environments.

For horses, with the notable exception of the Rochefort cave, the specimens of all the LGM and LG sites display a greater inter-individual variability (in anisotropy and complexity) than the archaeological populations of reindeer. The equines living before the LG generally adopted a generalist herbivore diet with the occasional grazer tendency. The specimens at level IV0 of Pincevent are also generalists, but with browsing tendencies. However, it is necessary to study other archaeological populations from the LG to establish whether this is an evolution in horses' diets over time.

At the inter-species level of variability (figs. 3, 4), our results are largely based on the two sites of the Rochefort cave and Pincevent (level IV0). During the LGM, at the Rochefort cave, feeding habits differ between species. Reindeer tend to be grazers, while horses are more often generalists with grazing tendencies. During the LG, on level IV0 in Pincevent, we can observe slightly different values from one species to the other. The reindeer are mixed feeders, whereas horses can be found between generalists and browsers. These species then selected some resources within the same habitats and thus came to share them partly (even if they ate the same plants in general, differences could have happened on plant parts, maturation, etc.; Guthrie, 1982). These results bolster the argument of plant resource partitioning, favoured by the mosaic landscape common to the ecosystems of the Mammoth Steppe. It is however useful to mention that the sharing of plant resources fluctuates over time, probably due to climate oscillations, but it can also be linked to palaeoenvironmental configurations at local or regional levels. Thus, for example, reindeer diet in Colombier, in Chézy-sur-Marne, has a signature that is very close to that of horses in the Rochefort cave and the Amiens-Renancourt 1. In addition, the climate instability of the LGM, involving rapid modifications in the distribution or disappearance of plant resources, may have had selective impacts on animal diets. These phenomena can only be understood with additional studies on dental microwear. Also needed – and currently in development – are isotopic analyses of bioapatite on a large number of modern and archaeological specimens to understand the climate and feeding variations throughout a single year (Catz, doctoral thesis, ongoing).



Finally, dental microwear texture analyses allow us to measure the dietary plasticity of the key Palaeolithic herbivores. Of even greater note, they offer additional information to palaeobotanic studies aimed at reconstructing plant communities, their coevolutionary ties with large herbivores, and the structuring of landscapes. Our results reinforce hypotheses relative to the existence of LGM cryptic refugia in northern regions of France and the geographical and chronological fluctuation of meta-communities (Bignon-Lau et al., 2019). Furthermore, the preferential, coevolutionary predator-prey ties that linked humans and the two preys horse and reindeer might have played a role in the ecological stability between the LGM and the LG, simultaneously favouring the specific structuring of the Mammoth Steppe and the relative heterogeneity of its landscapes (see discussion in Bignon-Lau, 2014; Bignon-Lau et al., *ibid.*).

Despite animal communities that seem to have remained diversified from the LGM to the LG, the remarkable recurrence of horse and reindeer hunts seems to be a trans-cultural marker in the northern half of France during these periods (Bignon-Lau, 2014). It should be noted that these preys have (1) a strong potential for mobility, and (2) an average corporal mass for large mammals. While the capacity for mobility constitutes an advantage for their survival in mosaic landscapes, it is also an opportunity for hunters to anticipate and organize various tactics. Several tactics observed during the LG (Bignon, 2008) are thus equally possible for the LGM (Bemilli and Hinguant, 2014), such as stalking herds along migration routes or collective hunts (interception, driving back) in

refuge zones or environments with the richest plant resources. After obtaining the prey, the latter's body mass lends itself to transporting carcasses or anatomic segments that are economically profitable. Thus, though the mobility of different cultural groups was not identical from the Solutrean to the Upper Magdalenian at the scale of the vast region, these human societies do share a significant logistical dimension. This is corroborated by the fact that, even during the LGM, the geological knowledge required to maintain flint supplies indicates that the territory was occupied more persistently than just during simple, furtive, northern incursions (Hinguant and Biard, 2013; Hinguant and Colleter, 2020). This extensive knowledge of territorial characteristics goes hand in hand with the understanding of prey and the rhythms of their movements, because the constant adjusting to their mobile resources was vital for these hunter-gatherer societies.

CONCLUSION

Dated bones from the LGM found in the north of France allow us to place the archaeological sites of the region in the environmental context of the Mammoth Steppe. Indeed, the presence of several taxa on these sites demonstrates the existence of a diversified animal community in these northern European zones. Furthermore, the sites in this study strongly suggest that LGM animal communities were viable resources for human societies, despite palaeoenvironmental and climate variations.

This in turn supports the hypothesis of the existence of cryptic refugia that may have sheltered, at least temporarily, both human societies and animal communities during many long months. If this is true, our research has laid the foundation for establishing the diet of the preferred key preys of human hunters during the LGM and LG. Indeed, our study offers new data that help (1) reconstruct the diet of reindeer and horses discovered at various sites during our period of study, and (2) gain a better understanding of palaeoecology in the Paris Basin at the end of the Upper Paleolithic.

Our first dental microwear texture analyses show that during the LG and even the LGM, plant resources seem to have been sufficiently abundant and diversified to maintain populations of large herbivores in the Paris Basin, at least temporarily. Both species studied seem capable of adopting different dietary habits both inter- and intra-specifically. This upholds the idea that they partitioned plant resources, thus encouraging human societies to constantly focus their hunting practices on these two primary preys.

With these promising first results, more extensive analyses of dental microwear texture have begun on modern reindeer and horses, as well as on dental remains at other Palaeolithic sites in order to pinpoint variations in diet between both of these species. Going forth, we would like to combine dental microwear texture analyses with other proxies such as intra-tooth carbon and oxygen isotope analyses. Stable oxygen and carbon isotopes of mammalian tooth enamel record ecological conditions and dietary preferences experienced by an individual during dental formation. Therefore, reconstructing annual variations of reindeer and horses ethology would allow us to confirm

or adjust the hypothesis of diet plasticity among these species observed in DMTA and collagen isotopic records in the Paris Basin during the LGM and the LG. Strontium isotope analyses would allow us to answer questions concerning the movement of these taxa within a region that was long considered too cold to shelter such diversified and complex communities. By better understanding biological, ecological, and climate mechanisms, we would be able to discover why and how these animal communities lastingly inhabited the northern zones of France.

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NOTES

- (1) Original quote: « [...] la vie ne saurait être seulement atomisée en organismes et cloisonnée en espèces : elle vit aussi éco-organisationnellement. L’évolution de la vie, c’est aussi l’évolution des écosystèmes, dans laquelle l’évolution des espèces est à la fois entraînée et entraînée. »

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