The Ice Age diet of the La Quina 5 Neandertal of southwest France / *Le régime alimentaire*

Néandertalien de La Quina 5 pendant la période glaciaire du sud-ouest de la France

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Abstract

The La Quina 5 Neandertal individual, dated to late Marine Isotope Stage (MIS) 4 or early MIS 3, lived during a particularly cold and arid Ice Age interval, hunting mostly reindeer in open steppe habitat. Stable isotopes indicate the importance of hunted resources for Neandertals, although evidence of plant use also has been discovered. To address the plant food signature in the diet of La Quina 5, we marshal multiple methods, including dental microwear texture analysis (DMTA) and plant microremains analysis. For the DMTA, La Quina 5 is compared to Neandertals from MIS 3 – MIS 5, including Malarnaud, Spy I, Kůlna 1, Švédův stůl 1, and several individuals from Vindija (n = 4), Hortus cave (n = 5) and Krapina (n = 19), as well as Holocene human foragers, farmers and pastoralists (n = 150). La Quina 5 presents a low value for anisotropy implying the use of heterogeneous masticatory regimes like those characterizing Holocene foragers. La Quina 5 also has a low complexity value indicating a plant-poor diet, and may have consumed foods that were processed less than other Neandertals and Holocene foragers as well as mid-Holocene abrasive food forager/farmers. La Quina 5 may have relied significantly on hunted resources perhaps necessary in the cold glacial interval of lower temperatures during Heinrich Stadial 6. Nevertheless, plant microremains are preserved in the dental calculus, including starch grains from grass seeds and plant underground storage organs, demonstrating the importance of plant foods in Paleolithic diets even if temporally or spatially dispersed.

Key words: dental microwear texture analysis; plant microremains; dental calculus; Marine Isotope Stage 4; paleoecology

Résumé

L'individu néandertalien La Quina 5, daté de la fin du stade isotopique marin (MIS) 4 ou du début du MIS 3, a vécu pendant une phase de la dernière période glaciaire particulièrement froide et aride, chassant principalement des rennes dans un habitat steppique ouvert. Les isotopes stables indiquent l'importance des ressources animales dans le régime alimentaire des Néandertaliens, bien que des preuves d'utilisation de plantes aient également été découvertes. Afin de mieux décrire la part végétale du régime alimentaire de l'individu La Quina 5, nous utilisons ici plusieurs méthodes, notamment l'analyse de la texture des micro-usures dentaires (DMTA) et l'analyse des microrestes végétaux. Pour l'analyse DMTA, La Quina 5 est comparée aux Néandertaliens du MIS 3 – MIS 5, dont Malarnaud, Spy I, Kůlna 1, Švédův stůl 1, et plusieurs individus de Vindija (n = 4), la grotte de l'Hortus (n = 5) et Krapina (n = 19), ainsi que des chasseurs-collecteurs, des agriculteurs et des éleveurs de l'Holocène (n = 150). La Quina 5 présente une faible valeur d'anisotropie impliquant des régimes masticatoires hétérogènes comme ceux caractérisant les chasseurs-collecteurs de l'Holocène. La Quina 5 a également une faible valeur de complexité indiquant un régime alimentaire pauvre en plantes, et qui pourrait indiquer la consommation d'aliments moins transformés comparativement aux autres néandertaliens, aux chasseurs-collecteurs de l'Holocène ainsi qu'aux collecteurs et agriculteurs consommateurs d'aliments abrasifs de l'Holocène moyen. La Quina 5 pourrait s'être reposé de manière significative sur les produits de la chasse, probablement par nécessité face aux conditions climatiques du stadiaire de Heinrich 6 aux températures particulièrement basses. Les micro-restes végétaux préservés dans le tartre dentaire démontrent cependant la présence de plantes dans les régimes alimentaires paléolithiques, même si leur importance a pu varier dans le temps ou dans l'espace.

Mots clés : analyse de la texture des micro-usures dentaires; microrestes végétaux; tartre dentaire; stade isotopique marin 4; paléoécologie

1. Introduction

Numerous dietary reconstructions have appeared since Neandertal dietary proclivities were first inferred using faunal remains (e.g., Lartet, 1875; Hrdlička, 1927; Binford, 1981). Recent reconstructions have incorporated innovative methodological approaches to infer diet, including analyses of residues on stone tools (B. Hardy, 2010) and in dental calculus (K. Hardy et al., 2012, Henry et al., 2011, 2014; Power et al., 2018), dental microwear texture analysis (El Zaatari et al., 2011, 2016; Karriger et al., 2016; Estalrrich et al., 2017; Williams et al., 2018, 2019, 2021), dental macrowear (Fiorenza et al., 2011) and isotopic analyses (Bocherens et al., 2001; Richards and Trinkaus, 2009; Wißing et al., 2016). The remains of small, medium, large and very large faunal remains with cut-marks at Neandertal sites serve as evidence of meat-eating while isotopic values like those of carnivores imply a meat-laden diet (Jaouen et al., 2019). Stone tool residues and the identification of plant remains in preserved dental calculus provide information about the kinds of plants that were processed and consumed. Studies of dental microwear and dental macrowear yield inferences regarding ecological habitat whereby variation in tree cover corresponds to the degree to which plant foods were available and exploited.

There is also much variation in the diet that signals adaptations corresponding to climatic changes that occurred during Marine Isotope Stages (MIS) 5 to 3 (Williams et al., 2018, 2019, 2021). The exact impact of global climate change on terrestrial ecosystems at these times is still hard to grasp, but appears highly variable geographically (Sánchez Goñi et al., 2008; Genty et al., 2010). Southwestern France was one of the core regions occupied by Neandertals throughout

MIS 5 to 3. They lived during a warm interglacial period (MIS 5) similar to that of extant western Eurasian habitats, before witnessing increasingly cool and dry environmental shifts from MIS 5 to MIS 4. Towards the end of MIS 4, approximately 63 to 60 ka before present (BP), the climate deteriorated further (Heinrich stadial 6), reducing the presence of Neandertals in northwestern Eurasia as the glaciers and tundra habitat expanded (Sánchez Goñi et al., 2008; Genty et al., 2010). However, in some areas of the continent, small groups of Neandertals apparently survived, including in the Charente area of southwestern France, a region of low elevation west of the Massif Central. At La Quina cave in Charente, a relatively uninterrupted depositional history is preserved throughout much of the deterioration of climatic conditions during the end of MIS 4 and the beginning of MIS 3. One of the most complete individuals recovered from La Quina cave is La Quina 5 (Henri-Martin, 1911, 1923). To explore how this older adult Neandertal survived in this relatively inhospitable habitat, we approach the dietary reconstruction of La Quina 5 using dental microwear texture analysis and an analysis of plant microremains preserved in the dental calculus.

2. Materials and Methods

2.1. Methodological considerations

2.1.1. Dental microwear texture analysis

Molar occlusion during mastication shears and grinds food as well as exogenous particles that enter the oral cavity. The resulting micro-topographical damage to the enamel surface forms surface characteristics that are studied via three-dimensional dental microwear texture analysis (El Zaatari et al., 2011, 2016; Scott et al., 2005, 2006, 2012; Krueger et al., 2008, 2019; Ungar et al., 2012; Schmidt et al., 2016, 2019, 2020). Several textural properties can describe the enamel

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surface. We focus on complexity and anisotropy to separate hard versus tough diets (Scott et al., 2005) (Fig. 1).

[Fig. 1]

2.1.1.1.   Complexity (Asfc)

Complexity, or Area Scale Fractal Complexity (Asfc) is a representation of surface relief calculated at multiple scales. An enamel surface that is relatively complex exhibits features of various sizes and depths. Higher complexity (Asfc) values are associated with feeding on hard objects such as phytoliths, seeds, seed casings, shells and other plant parts as well as windborne and terrestrial grit (Scott et al., 2005, 2006, 2012; Schmidt et al., 2016, 2019; Calandra et al., 2012; DeSantis et al., 2018). A less complex surface would consist of fewer features with minimal contrasts of elevations. Low values have been suggested to correspond to diets heavily reliant on foods such as meat that do not abrade the enamel (Hua et al., 2015).

2.1.1.2.   Anisotropy (epLsar)

The texture of the enamel surface also can be described in terms of exact proportion length-scale anisotropy of relief, or epLsar. Surfaces having their features aligned in a similar orientation are termed anisotropic; high anisotropy values derive from jaws moving in similar directions and tend to be found in human groups (and non-human primate species) eating tough foods, such as leaves, stems, grasses, root ends or other foods with structural carbohydrates that must be reduced by chewing in the same direction (Scott et al., 2006; Schmidt et al., 2019). Low anisotropy occurs when a varied diet necessitates heterogeneous jaw movements, resulting in features that are positioned without a preferred directionality (Fig. 1). In humans, groups that eat large quantities of hard but brittle foods, like seeds and nuts, tend to have lower anisotropy values.

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2.1.2. Methodological context for plant microremain identifications in dental calculus

Dental calculus, or mineralized oral plaque, is increasingly used as a source of information about past human behavior, including for Neandertals (Henry et al., 2011, 2014; Hardy et al., 2012; Power et al., 2018). As it forms, dental calculus incorporates elements of the oral cavity, including residues of food, into a hard mineral matrix where it is preserved over archaeological time scales. While multiple kinds of residues can be recovered from calculus, we focus on plant microremains, as these provide the most direct evidence of the consumption of plant foods. Plant microremains are microscopic particles of plants that preserve taxon-specific morphology, and that can be identified through comparison to modern reference material. Here we examined two plant microremains: starch grains and phytoliths. Starch grains are semicrystalline structures made from amylose and amylopectin, two kinds of glucose polymers that plants produce as a means of long-term energy storage. They are often located in the parts of plants that are targeted by human consumers, such as the seeds (e.g., nuts) and underground storage organs (e.g., tubers). Phytoliths are silica bodies that are often found in the exterior tissues of plants, such as the leaves, husks, and rinds, and are thought to be produced as a means of structural support or physical defense.

2.2. La Quina 5 preservation, stratigraphic context and dating

2.2.1. La Quina preservation and dental characteristics

La Quina 5 includes a nearly complete calvarium, lower maxilla and mandible, as well as several postcranial elements, including both humeri and femora, as well as a virtually complete left radius and ulna that were discovered after the publication of Henri-Martin's 1923 monograph (Trinkaus, 2016). Originally, La Quina 5 was described as a female Neandertal (Henri-Martin, 1911, 1923). However, Trinkaus (2016) disagrees, assigning the fossil to male or indeterminate.

Given the low antebrachial index of La Quina 5, which is significantly smaller in human females compared to males (Williams et al., 2015), we assign this individual to female or indeterminate.

The teeth are worn to a single functional plane. The remaining severely worn maxillary incisors, right I^1 and left I^2, with dental wear scores of 5 and 6, respectively (Smith, 1984) suggest the anterior dentition of La Quina 5 was intensively utilized. The mandibular incisors and right canine are absent, but the left mandibular canine and maxillary canines, with dental wear scores of 4-5 (Smith, 1984), exhibit greater attrition than the premolars. Asymmetrical dental wear is present with the right showing greater attrition for both the maxillary and mandibular postcanine dentition. The lower left M_1, with a dental wear score of 5 (Smith, 1984) exhibits thick enamel ribbons along the periphery and large enamel islands with well-preserved dental microwear. The considerable dental wear suggests La Quina was an older adult. There was very little calculus present, with very small deposits on the distal surfaces of the lower left and right third molar and the right upper third molar.

2.2.2. La Quina 5 stratigraphic context

The La Quina 5 Neandertal skeleton comes from the La Quina "Station Amont" Mousterian sequence (Fig. 2). It was discovered the 18th of September 1911 by L. Henri-Martin during his excavations (1905-1936) at the site. Later excavations by G. Henri-Martin (1953-1972) and A. Débenath & J. Jelinek (1985-1995) considerably improved our understanding of the stratigraphy, and the nature and dating of the "Station Amont" cultural levels of occupation (Henri-Martin, 1911, 1923; Debénath and Jelinek, 1998). La Quina 5 skeleton was described by L. Henri-Martin as coming from his "couche 3", in trench B (Henri-Martin, 1911, 1923). This can be correlated to layers L to Q (and potentially N) from the new excavations, corresponding

to Quina Mousterian occupations (Bourguignon, 1997; Debénath and Jelinek, 1998; Verna, 2006; Jelinek, 2013).

[Fig. 2]

2.2.3. La Quina cave dating

Henri-Martin's "couche 3", which yielded La Quina 5, cannot be correlated to a specific layer or absolute date, but broadly corresponds to the Mousterian Quina layers uncovered at the site. Levels 8 to 2a from recent excavations, above the Quina Mousterian layers, were estimated to date to 48.17-42.53 ka BP using a Bayesian model based on radiocarbon and luminescence dates (Higham et al., 2014), but this model has been strongly criticized (Discamps et al., 2015). Luminescence dates recently published (Frouin et al., 2017) placed the Quina Mousterian layers of La Quina around 55 to 63 ka cal. BP. Biochronological data for the Quina Mousterian macro- and microfauna of southwestern France suggests a date corresponding to Heinrich stadial 6, circa 60-63 ka BP (Genty et al., 2010; Discamps and Royer, 2017), in agreement with the luminescence dates of Frouin et al. (2017).

2.3. Comparative samples for the dental microwear texture analysis

2.3.1. Comparative Neandertal sample

To provide a context for La Quina 5, Neandertals from Mediterranean and continental ecogeographic zones were included. During MIS 3, the Mediterranean zone was somewhat warmer and more arid than inland continental areas, but exhibited much variability, including some severe cold and arid periods (Pillard, 1972; H. Lumley, 1972; Lumley and Licht, 1972; M. Lumley, 1973. We sampled five individuals from Hortus cave ~30 km north of the coast, including Hortus V and Hortus VIII from Phase Vb, which was the coldest and most arid of the sequence as well as the most recent; Hortus XI from Phase Va, which was slightly less cold;

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Hortus IV from Phase IVb which was the least cold and dry as well as the earliest; and Hortus VI which was retrieved from the cave infill; all phases of the Hortus assemblage are dated to MIS 3 (H. Lumley, 1972; Lumley & Licht, 1972; Pillard, 1972; M.-A. Lumley, 1973; Lebègue et al., 2010; Williams et al., 2018).

In MIS 3, continental sites of north and central Europe where more forested than the Mediterranean region, with conifers and mixed/patchy woodlands as well as open tundra habitats (Fiorenza et al., 2015). From this zone we included Kůlna 1 and Švédův stůl 1 (Ochoz 1) from the Czech Republic, dated to MIS 3 (Neruda and Nerudová, 2014; Nerudová et al., 2014) as well as Spy I from Belgium, dated to ~36 ka BP on the basis of radiocarbon dates for Spy I (94a) (35,810 + 260–224 years BP) and Spy II (92b) (36,350 + 310–228 years BP) (Semal et al. 2009). At the terminus of MIS 3, Spy cave was a cold-wet region at the northern fringe of habitable conditions for Middle Paleolithic peoples (Semal et al. 2009, 2011, 2013). From the warmer last interglacial (MIS 5), we included Malarnaud from the piedmont of the Pyrenees of France (Petite-Marie et al., 1971).

To provide additional comparative Neandertal samples, the means and standard deviations from isolated Krapina (n = 19) and Level G Vindija (n = 4) molars were included (Karriger et al., 2016). Krapina is dated to 130 ka ± 10 ka BP corresponding to MIS 5e (Rink et al., 1995), and is reconstructed as a warm interglacial interval. Level G3 of Vindija is dated to MIS 3 and is older than 42 ka BP (Wild et al., 2001; Karriger et al., 2016). The Neandertals at Vindija experienced a colder habitat than those at Krapina. The Level G deposits from Vindija record a temperate habitat of forests, open areas and grasslands (Miracle et al., 2010).

2.3.2. Comparative human samples

Additional comparative samples derived from the published dental microwear texture complexity and anisotropy values for seven human groups (n = 150). Since similar dental microwear textural characteristics can result from the mastication of a wide variety of resources, both wild and domesticated, we consider the mechanical properties of the foods consumed rather than any specific dietary item when comparing Epipaleolithic and Holocene human groups to Neandertals from MIS 5-3. The human samples were chosen to typify some of the major differences among known human subsistence patterns. For example, human foragers and food producers tend to exhibit distinctions in diet (Schmidt et al., 2019). Hunter-gatherers of the New World consumed harder foods that were much coarser compared to, for example, pastoralists of the Mongolian steppe (Schmidt et al., 2016, 2019). In addition, farmers and herders exhibit a greater uniformity of jaw movement leading to higher anisotropic values compared to foragers (Schmidt et al., 2016, 2019).

2.3.2.1. Foragers

Hunter-gatherers from Eurasia and the Americas were considered. We added Epipaleolithic sedentary Natufian foragers from Israel (n = 15) to the sample, dated to 14-10 ka BP (Fagen, 1995; Karriger et al., 2016). Natufian subsistence included hard seeds, nuts, copious grains, tough and unprocessed foods as well as wild gazelle (Fagen, 1995; Karriger et al., 2016). Their dental microwear textures, however, look more like farmers than foragers, which speaks to their great reliance on grains (Schmidt et al., 2019). From the Americas, we included Paleoamerican foragers from Lagoa Santa, Brazil (n = 23) dated to 11-7 ka BP (Da-Gloria and Schmidt, 2020). The subsistence record of the Lagoa Santa foragers included a varied diet comprising fruits, grass seeds, roots and small-medium sized animals (Da-Gloria and Schmidt, 2020). We included hunter-gatherers with some domesticates from the Archaic period of Indiana

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(n = 34) and Archaic Kentucky (n = 13), dated to 2.5 ka and 3 ka BP, respectively (Yarnell, 1993; Jefferies, 2009; Frazer, 2011; Karriger et al., 2016; Schmidt et al., 2020), characterized as hard-food foragers with an abrasive diet of poorly processed wild foods such as nuts, occasionally supplemented with domesticates including seeds and leaves of chenopods, knotweed, sumpweed and goosefoot as well as deer, rabbit, fish, shellfish, birds and other animals (Yarnell, 1993; Fagen, 1995; Jefferies, 2009; Frazer, 2011; Karriger et al., 2016; Schmidt et al., 2020).

2.3.2.2. Farmers and pastoralists

We added three food producing societies from Karriger et al. (2016) that serve as a contrast to hunter-gatherers from the Holocene, Epipaleolithic and Late Pleistocene. To include a diet with little evidence of wild foods, we chose Early Bronze Age England (n = 21) from the Beaker period, 4.5 ka BP to 3.5 ka BP and Late Bronze/Early Iron Age Greece ~3.5-2.9 ka BP (n = 15) (Chiu et al., 2012; de Gregory, 2012; Dickinson, 2006). Both societies depended on Near East domestics of wheat, barley, sheep, goats and cattle, although Early Bronze Age England may have exhibited a coarser diet than Bronze/Iron Age Greece, perhaps due to poor processing (Fagen, 1995; Chiu et al., 2012; de Gregory, 2012; Dickinson, 2006). We included Xiongnu pastoralists from Mongolia (n = 49) Late Bronze/ Early Iron Age to demonstrate the complexity and anisotropy of a plant-poor diet rich in meat and animal products. Xiongnu pastoralists traded millet with farmers for meat and hides but otherwise included few plant foods in the diet (Machicek and Zubova, 2012; Murphy et al., 2013).

2.4. Microscopy, scanning and data reduction

A polyvinylsiloxane replica of the left M_1 of La Quina 5 was created by FLW at the Museé de l'Homme (Paris) using President Plus (Coltène-Whaledent) regular body impression

material. Dental molds were also created for Malarnaud at the Museé de l'Homme, and Hortus IV, Hortus V, Hortus VI, Hortus VIII and Hortus XI at the Centre Européen de Recherches Préhistoriques de Tautavel. A dental mold of Spy I was loaned to FLW by Patrick Semal of the Royal Belgian Institute of Natural Sciences, Brussels. Epoxy resin (Buehler) dental cast were created at Georgia State University. Values for Kůlna 1 and Švédův stůl 1 were obtained previously (Williams et al., 2019, 2021).

All of the dental casts were scanned using the "Indie" machine at the University of Indianapolis. By using the same protocol and software the confounding problems associated with comparing data across institutions/devices was avoided (Arman et al., 2016). We used a white-light confocal profiler (Sensofar Plµ) at 100x magnification on Phase II facets, focusing on facet 9 (Kay and Hiiemae, 1974; Krueger et al., 2018). Four adjacent scans were stitched together digitally, for a total study area of 242 x 182 for each of the individuals. The scanned data clouds representing the total study areas were then uploaded into SolarMap 5.1.1. This program allowed the scans to be leveled and permitted surface cleaning, where the analyst removes all surface particles from the data. Prior to analysis, two and three-dimensional surface reconstructions were created to examine whether postmortem taphonomic factors such as casting defects, chemical adherents or preservation artifacts, were present (Fig. 3).

[Fig. 3]

2.5. Plant microremains analysis

2.5.1. Calculus sampling, preparation and analysis

The dental calculus samples from La Quina 5 were collected at the Museé de l'Homme in the spring of 2008 by AGH. The teeth were photographed before and after sampling, and the calculus surface was gently wiped with an alcohol swab to remove surface contaminants. The

calculus was removed from the distal surfaces of the lower left and right third molars and upper right third molar, using a dental scalar. The calculus from each tooth was collected into separate 1.5ml microcentrifuge tubes and transported to the Archaeobiology Laboratory at the Smithsonian Institution's Museum Support Center. There they were lightly ground using a plastic pestle designed to fit directly into the tubes, mounted in distilled water, and directly examined under a transmitted light microscope with cross-polarization and attached camera at 400x magnification. Note that significant improvements have been made to the methods of calculus sampling since this material was collected, including better contamination controls (Crowther et al., 2014) and the use of EDTA instead of grinding (Tromp et al., 2017).

2.5.2. Identification based on comparison to reference collection of modern plants

The recovered microfossils were identified based on comparison to a reference collection of over 1000 plant taxa. The identification relies on shared diagnostic morphology, including the overall shape of the microremain, and presence and appearance of internal structures including hila, lamellae, and fissures in the case of starches. The initial study of the microremains in the La Quina 5 calculus were presented in Henry (2010) and Henry et al. (2011). In this study, these results are interpreted in light of newly available data from analysis of dental calculus residues from other Neandertal specimens.

3. Results

3.1. Complexity and anisotropy of La Quina 5 compared to Neandertal assemblages and sites

In comparison to other Neandertals, La Quina 5 exhibits a relatively low value for complexity (Fig. 4). La Quina 5 falls entirely outside of the convex hull for the Hortus assemblage, and is distinct from Kůlna 1 and Spy 1 with much higher complexity values. For complexity, La Quina 5 is the most similar to Švédův stůl 1, Malarnaud, and Hortus V but

exhibits a lower value than all of them. La Quina 5 approximates the value of Krapina 9 and

Krapina 165. Although the complexity of La Quina 5 is quite low (0.794493), five individuals

from Krapina (135, 136, 167, 173 and 172) and two individuals from Vindija (11.39 and 12.1)

present even lower values (Fig. 4). La Quina 5 is nestled within the convex hull demarcated by

the Krapina and Vindija assemblages, particularly the latter site (Fig. 4).

The anisotropy value for La Quina 5 (0.002383) is also low and is most similar to that of

Švédův stůl 1, Hortus XI and Krapina 135. It should be noted that both Švédův stůl 1 and Hortus

XI, like La Quina 5, can be described as older adults. The young adults from Hortus cave,

including Hortus IV, Hortus V, Hortus VI and Hortus VIII exhibit much higher anisotropy.

These values are surpassed by seven isolated molars from Krapina. In fact, 16 out of 19

individuals from Krapina present higher anisotropy values than La Quina 5 (Fig. 4). With respect

to Vindija, the anisotropy of La Quina 5 is most similar to Vindija 11.40. La Quina 5 is

decidedly unlike Vindija 11.39 and Vindija 11.45 with extremely low anisotropy and Vindija

12.1 with a highly elevated value (Fig. 4).

[Fig. 4]

3.2. La Quina 5 compared to the 95% confidence intervals of the comparative samples

  3.2.1.   Complexity

La Quina 5 falls within the 95% confidence interval for Vindija but not for Hortus and

Krapina (Fig. 5). Compared to human foragers, La Quina 5 presents a low value and falls outside

of the 95% confidence interval for all of them with the exception of Xiongnu herders from

Mongolia with plant poor diets. La Quina 5 is distinct from the paleoforagers of Lagoa Santa

Brazil, characterized by particularly hard and abrasive diets (Fig. 5).

  3.2.2.   Anisotropy

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The anisotropy of La Quina 5 is also low and falls completely outside of the 95% confidence intervals for Hortus and Krapina (Fig. 5). However, the value for La Quina 5 approximates the mean for Vindija. La Quina 5 is most similar to human foragers from the Americas, particularly Archaic Indiana. The relatively low anisotropy of La Quina 5 is typical of human foragers and is unlike human food producers with much higher anisotropy values (Fig. 5).

[Fig. 5]

3.3. Plant microremains analysis

Very few microremains were recovered from the three calculus samples. Two definite starches and one possible starch were recovered (Fig. 6). All three showed signs of damage, including cracking and distortion of the polarization cross, and all three were heavily encrusted with calculus material. The first starch is circular in plain view and biconvex in side view; overall it is lenticular. It also has a central depression, and wide, diffuse arms and center in the polarization cross, with a small area at the hilum that retains a good degree of polarization. Given these features, this starch is consistent with starches of the Triticeae, the tribe of plants that contains wheat, barley, goat grass, and their wild relatives (Fig. 6). Based on its ovoid form, eccentric hilum that is located closer to the narrow short end, and faint lines extending from the hilum toward the opposite margin, we identify the second starch as consistent with those from plant underground storage organs (Fig. 6). The third object slightly polarizes but appears broken in half.

[Fig. 6]

4. **Discussion**

4.1. Environmental proxies for late MIS 4 and early MIS 3

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Prior to late MIS 4, Neandertals from southwest France mainly hunted red and roe deer, with a much smaller presence of bovids and equids (Discamps and Royer, 2017). In Charente and Périgord, during the Quina Mousterian, reindeer (*Rangifer tarandus*) most often represented more than >70% of hunted ungulate bones (Discamps and Royer, 2017). This is true for La Quina and surrounding sites (only assemblages with a total ungulate NISP >100 are discussed in the following): Les Pradelles [72-91% (Costamagno et al., 2005)], Jonzac Chez-Pinaud [77-90% (Airvaux, 2004; Niven et al., 2012), Roc de Marsal [82-85% (Castel et al., 2017)] and Pech de l'Azé IV [83-91% (Niven, 2013)], with relatively lower values at Hauteroche [57% (Paletta, 2005)] and Combe Grenal [48-71% (Guadelli, 1987)], but see (Discamps and Faivre, 2017) for a discussion on the impact of recovery bias on reindeer proportions. The faunal remains uncovered in the Quina Mousterian layers from the La Quina Station Amont have not been fully studied, hence it is not possible to compare quantitative data, but several sources point to a very large proportion of reindeer in the hunted spectra (Henri-Martin, 1923; Armand, 1990; Jelinek, 2013). Reindeer are biologically adapted to extreme cold, but they are a highly plastic species that can occupy tundra, taiga, or forested mountainous regions (Geist, 1998).

The preferential preservation of small mammals associated with cold and arid climates, such as narrow-headed voles (*Microtus gregalis*) and arctic lemmings (*Dicrostonyx torquatus*) found in tundra habitats and adjacent areas from Siberia to Alaska, corroborate the inference of lower temperatures and the presence of grasslands. Models based on micromammal communities point to dry soil conditions, and an arctic biome with shorter temperate intervals (Discamps and Royer, 2017).

Mammalian communities surrounding La Quina cave record a climate shift as the environment deteriorated with the onset of severe conditions at the end of MIS 4, known as the

Villars cold phase (68 to 61 ka BP) and the Heinrich stadial 6 (63.27-60.94 ka BP) (Genty et al., 2010). The emergence of cold and arid conditions resulted in broadleaf and temperate forests rapidly giving way to open grassland habitats as deduced by pollen from marine cores and stalagmites (Genty et al., 2010; Discamps and Royer, 2017).

At Villars cave, stalagmites provide evidence of sharp cold Heinrich stadials, extreme in terms of dryness. Pollen remains during the Heinrich stadials include *Pinus* as well as semi-desert Mediterranean taxa interdigitated with evidence of warmer and wetter temperate conditions (Sánchez Goñi et al., 2008; Genty et al., 2010; Discamps and Royer, 2017). During the Heinrich events, Villars cave stalagmites record an increase in carbon values signaling reductions of pollen from Atlantic forest trees, such as deciduous oaks (*Quercus*), beech (*Fagus*), birch (*Betula*), hazel (*Corylus*) and hornbean (*Carpinus*) (Genty et al., 2010).

If the paleoenvironments at the time of La Quina 5 corresponded to cold conditions, they might still have included wooded areas with edible plant resources. Many of these edible plants could have derived from Atlantic forest products, including acorns and hazelnuts. Marine pollen cores from the Bay of Biscay demonstrate that although the Atlantic forests diminish greatly during late MIS 4 and early MIS 3, they never entirely disappear (Genty et al., 2010; Discamps and Royer, 2017). Stands of vegetation could have persisted next to bodies of water, including lakes, rivers and streams, and these could have been exploited heavily by the Mousterian reindeer hunters and plant gatherers of La Quina cave, particularly during the summer months and prior to the onset of the glacial winters.

4.2. Plant microremains and microwear texture patterning vis-à-vis environmental proxies

The number of plant microremains recovered is very low, and the identifications therefore tenuous. Microremains cannot be used to determine the proportions of plant and animal

foods; they simply record the presence of plants, or of different kinds of plants, in the oral cavity. La Quina 5, despite likely relying heavily on animal-derived foods, also consumed a number of different type of plants, including starch-rich grass seeds and plant underground storage organs. This pattern is similar to that observed across a large number of Neandertals, from a wide range of habitats across Eurasia (Power et al., 2018; Salazar-García et al., 2021). Though a few Neandertals from warmer regions or climatic periods have greater numbers of plant microremains preserved (e.g., Shanidar III and Spy I and II; 7), there is no consistent pattern suggesting that Neandertals in certain times or places consumed a larger number of plants than others (Power et al., 2018).

4.3. Comparison of La Quina 5 and Spy I

The sample from La Quina 5 had USO-type starches that were similar to what was found Spy I [6]. However, the number of recovered starches on Spy (n = 136) was much higher than on La Quina (n = 3), and therefore the identifications much more certain (48 versus 1, respectively). At Spy, plant microremains from underground storage organ of Nympheae (water lilies) and grass seeds of the Andropogoneae or Paniceae tribes were identified (Henry et al., 2011), corroborating the common use of starches from plant storage organs and grass seeds by Neandertals from the Iberia Peninsula to Siberia (Power et al., 2018; Salazar-García et al., 2021).

With respect to microwear texture, Spy 1 exhibits an elevated value for complexity suggesting greater use of plant foods in the diet (Williams et al., 2019). In contrast, the much lower value observed in La Quina 5 implies fewer plants were exploited. The paleoecology of Spy I at 36 ka BP in northwest Europe (Belgium) was reconstructed as an open habitat but with patches and microenvironments of plants, including oaks and other nut-bearing trees, as well as chenopods, grasses and plant storage organs (Semal et al., 2011; Williams et al., 2019). The

environment of La Quina cave during the terminus of MIS 4 and the beginning of MIS 3 was colder still with abundant reindeer. These constraints can also be applied to interpreting the dearth of plant microremains in La Quina 5 which strongly support the DMTA data. The low anisotropy of La Quina 5 could signal a plant-poor diet, but could also correspond to the consumption of relatively coarse foods that were only minimally processed. The rudimentary processing technology could also be inferred from the considerable asymmetric macrowear on the molars and the severe attrition and tooth loss of the anterior dentition of La Quina 5. The peculiar nature of La Quina 5 DMTA signal may also be explained by particular food processing techniques of animal products. For example, some zooarchaeologists have proposed the consumption of crushed spongy bone by Neandertals (Marean, 2005; Costamagno, 2013; Castel et al., 2017), as described for some native populations (Schaefer and Steckle, 1980).

4.3. Conclusion: What was the Ice Age diet of La Quina 5?

La Quina 5 lived during an inhospitable climate extreme in which survival hinged on the availability of animal resources. The heavy use of hunted returns is amply supported by the faunal remains accumulated by Quina Mousterian people in southern and western France, as well as isotopic analyses and comparisons of dental wear with recent foragers (El Zaatari et al., 2011; Fiorenza et al., 2011; Discamps and Royer, 2017; Jaouen et al., 2019). From the enamel textural complexity of La Quina 5, it can be inferred that fewer plants were consumed compared to other Neandertals, even those living farther north and east and this supposition is supported by the relatively small number of starch grains and phytoliths preserved in the dental calculus of the La Quina sample (Henry et al., 2011). Although heavily dependent on meat, plant underground storage organs and grass seeds were nevertheless exploited, probably for their essential

micronutrients. The low anisotropy of La Quina 5 signals that these plant parts were likely masticated using diverse, rather than uniform, movements of the jaws.

Acknowledgments

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Figure captions

Fig. 1. Idealized example of (a) complex (Asfc) and (b) anisotropic (epLsar) surfaces / Exemple

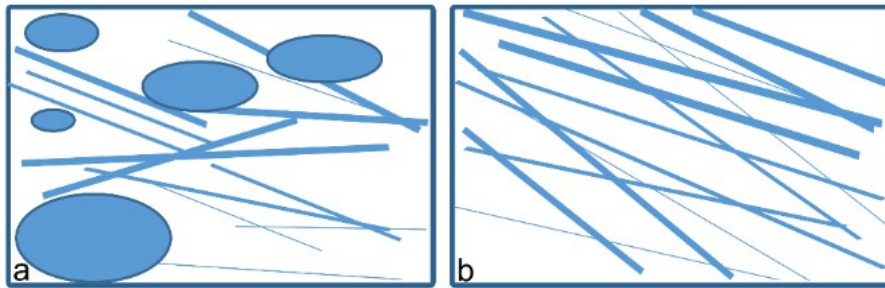idéalisé de surfaces (a) complexes (Asfc) et (b) anisotropes (epLsar)

Fig. 2. Map of western Europe with location of La Quina cave, as well as some Mousterian

Quina regional sites and paleoenvironnement proxies discussed in the text / Carte de l'Europe

occidentale avec emplacement de la grotte de La Quina, ainsi que certains sites régionaux du

Moustérien de Quina et des proxys paléoenvironnementaux discutés dans le texte

Fig. 3. Molar enamel surface reconstructions of La Quina 5 in two (a) and three (b) dimensions / Reconstructions de la surface de l'émail molaire de La Quina 5 en deux (a) et trois (b) dimensions
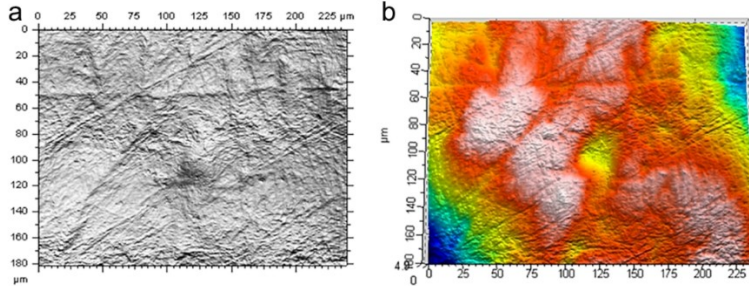

Fig. 4. Comparison of complexity and anisotropy in La Quina 5 (red circle) and other Neandertals, including Spy I (light-blue left-pointing triangle), Švédův stůl 1 (green right-pointing triangle), Kůlna 1 (orange triangle), Malarnaud (yellow-green inverted triangle), Hortus (teal stars), Krapina (dark green diamonds) and Vindija (blue squares)

Comparaison de la complexité et de l'anisotropie chez La Quina 5 (cercle rouge) et d'autres Néandertaliens, y compris Spy I (triangle bleu clair pointant vers la gauche), Švédův stůl 1 (triangle vert pointant vers la droite), Kůlna 1 (triangle orange), Malarnaud (triangle inversé jaune-vert), Hortus (étoiles bleu sarcelle), Krapina (losanges vert foncé) et Vindija (carrés bleus)
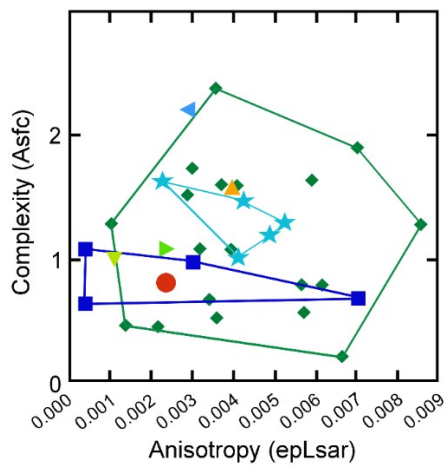
Fig. 5. Comparison of La Quina 5 (yellow) and the 95% confidence intervals for Neandertal assemblages (blue), foragers (red), farmers (green) and pastoralists (teal) for complexity (a) and anisotropy (b) Comparaison de La Quina 5 (jaune) et des intervalles de confiance à 95 % pour les assemblages néandertaliens (bleu), les butineurs (rouge), les agriculteurs (vert) et les éleveurs (sarcelle) pour la complexité (a) et l'anisotropie (b)
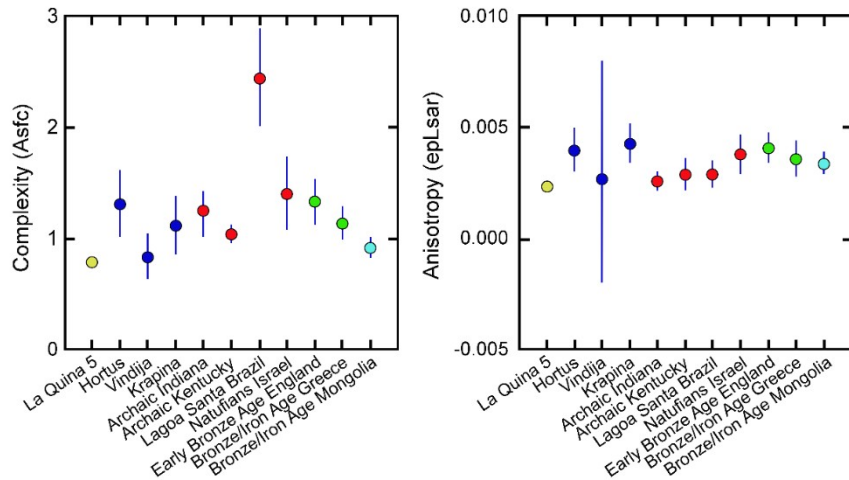

Fig. 6. Archaeological starch grains recovered from La Quina 5 calculus compared to modern reference material. Top two rows: starch grains recovered from the La Quina 5 calculus sample. Bottom two rows: modern reference material. One of each image pair is under brightfield and the other under cross-polarized light. a&b) probable Triticeae starch grain, c&d) probably plant underground storage organ starch, e&f) possible highly damaged starch, g&h) starch grain from modern *Triticum turgidum* subsp. *carthlicum* (a type of emmer), i&j) starch grain from modern *Nymphaea alba* (white water lily). All boxes are 50 µm on a side. / Grains d'amidon archéologique récupérés du calcul de La Quina 5 par rapport au matériau de référence moderne. Deux rangées du haut : grains d'amidon récupérés de l'échantillon de calcul de La Quina 5. Deux rangées du bas : matériel de référence moderne. L'une de chaque paire d'images est sous fond clair et l'autre sous lumière à polarisation croisée. a&b) grain d'amidon probable de Triticeae,

c&d) amidon d'organe de stockage souterrain probablement végétal, e&f) amidon possiblement très endommagé, g&h) grain d'amidon de Triticum turgidum subsp. carthlicum (un type d'amidonnier), i&j) grain d'amidon de Nymphaea alba moderne (nénuphar blanc). Toutes les boîtes mesurent 50 µm de côté.