



Human Palaeontology and Prehistory (Palaeoanthropology)

Dietary reconstruction of Spy I using dental microwear texture analysis



Reconstitution de l'alimentation de Spy 1 grâce à l'analyse de la texture des micro-traces dentaires

Frank L'Engle Williams^{a,*}, Christopher W. Schmidt^b, Jessica L. Droke^c,
John C. Willman^{d,e}, Patrick Semal^f, Gaël Becam^g,
Marie-Antoinette de Lumley^{g,h}

^a Department of Anthropology, Georgia State University, 30303 Atlanta, GA, USA

^b Department of Anthropology, University of Indianapolis, Indianapolis, IN, USA

^c Department of Anthropology, University of Wyoming, Laramie, WY, USA

^d IPHES, Institut Català de Paleocologia Humana i Evolució Social, Tarragona, Spain

^e Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Tarragona, Spain

^f Scientific Service of Heritage, Anthropology and Prehistory, Royal Belgian Institute of Natural Sciences, Brussels, Belgium

^g UMR 7194 CNRS, HNHP, MNHN/UPVD/CERP de Tautavel, Université de Perpignan, Perpignan, France

^h Institut de paléontologie humaine, Paris, France

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ABSTRACT

Spy I from the Meuse River Basin of Belgium is among the most recent Neandertals. This adult lived at the terminus of Marine Isotope Stage (MIS) 3 in cold steppe environments at the northern edge of the habitable zone for Neandertals where plants were relatively scarce. The dietary proclivities of Spy I are reconstructed using dental microwear texture analysis and compared to 33 Neandertals from western Eurasia, MIS 5 to MIS 3. Spy I has an elevated enamel surface complexity suggesting coarse dietary items such as wild seeds, acorns, nuts, and underground storage organs laden with particles of grit. Unlike the young and old individuals from Hortus with low values for anisotropy, Spy I is closest to the adults from this site suggesting a common pattern of masticatory behavior typified this life cycle stage. Like many other Neandertals, Spy I probably consumed plant foods at appreciable levels, some of which were hard and brittle or poorly processed.

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R É S U M É

Spy I provient du bassin de la Meuse en Belgique et fait partie des Néandertaliens les plus récents. Cet adulte date de la fin du stade isotopique marin (SIM) 3 et vivait dans des environnements de steppe froide, à la limite nord de la zone habitable pour les Néandertaliens, où les plantes étaient relativement rares. Le régime alimentaire de Spy I a été reconstitué en utilisant l'analyse de la texture des microtraces d'usure dentaires, comparées à celles d'un échantillon de 33 Néandertaliens européens, datant du SIM 5 au SIM 3. Spy I présente la plus

* Corresponding author at: Department of Anthropology, Georgia State University, 33, Gilmer Street, 30303 Atlanta, GA, USA.
E-mail address: frankwilliams@gsu.edu (F. L'Engle Williams).

haute complexité de l'échantillon néandertalien, suggérant la consommation d'aliments grossiers tels que des graines sauvages, des glands, des noix et d'autres matières stockées sous terre et chargées de particules de sable. Contrairement aux jeunes et adultes datés de l'Hortus, lesquels présentent une faible anisotropie, Spy I est le plus proche des adultes de ce site, ce qui suggère un schéma commun de comportement masticatoire caractéristique de cette étape du cycle de vie. Comme beaucoup d'autres Néandertaliens, Spy I a probablement consommé des aliments d'origine végétale à des niveaux appréciables, dont certains étaient durs et cassants ou mal transformés.

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1. Introduction

Spy I is from the tributaries of the Meuse River in Belgium (Fig. 1), and lived at the terminus of Marine Isotope Stage (MIS) 3 in the northernmost boundary of the Neandertals, above 50° N (Rougier et al., 2016). The region inclusive of present-day Belgium never experienced glaciation during the Upper Pleistocene unlike the Netherlands, Britain and Germany, and the varied landscape and presence of lithic outcroppings allowed for Neandertals to effectively exploit the region (Daujeard et al., 2016; Di Modica et al., 2016). However, during the terminus of MIS 3, the Meuse River Basin of Belgium experienced severe cold and aridity leading up to the Glacial Maximum at ~29,000 years (van Andel, 2002; Van Meerbeeck et al., 2009, 2011). This cold steppe habitat may have constrained the diets of Neandertals in the region. In this study, we reconstruct the dietary proclivities of a late surviving adult Neandertal, Spy I, living in one of the harshest habitats experienced by prehistoric humans of MIS 3.

1.1. Spy cave

Spy cave, or Li Bêch-aus-Rotches (Jemeppe-sur-Sambre), was inhabited more or less continuously from MIS 5e to MIS 3 (Semal et al., 2011, 2013; Toussaint et al., 2011; Fig. 1), excepting a 4000-year hiatus of anthropogenic activity during MIS 4 (Daujeard et al., 2016). The commanding view of the surrounding countryside and the range of microhabitats such as uplands, ravines and rivulets from which local resources could be procured contributed to the attractiveness of Spy cave as a habitation site (Daujeard et al., 2016; Semal et al., 2013). Fossils were discovered at Spy cave in 1886 and excavation of two adult Neandertals (Spy I and Spy II) provided evidence that the Feldhofer 1 remains were part of a larger entity known now as the Neandertals (Semal et al., 2013). Furthermore, Spy cave documented the first occurrence of Neandertal remains found *in situ* with ice age fauna and Mousterian tools (Semal et al., 2013).

The two adults include gnathic remains with associated dental elements, as well as relatively complete calvaria and multiple post-cranial elements. A maxillary fragment with a right M₃ *in situ* from Spy I (94a) is radiocarbon dated to 35,810 ± 260, -224 years BP (Semal et al., 2009), and a left I₁ (92b) of Spy II is dated to 36,350 ± 310, -228 years BP (Semal et al., 2009). These dates are consistent with the artifact assemblage and paleofauna. Calibrated dates suggest 39 kya BP (Crevecoeur et al., 2010). Based on radiocarbon

dating, the Spy adults are more likely to be associated with the second fauna bearing level that includes Late Mousterian and transitional Lincombian Ranisian Jerzmanowician artefacts, rather than the third fossiliferous unit (Semal et al., 2009).

1.2. Prior dietary reconstructions

Neandertal dietary behavior has been explored previously (El Zaatari et al., 2011, 2016; Estalrriich et al., 2017; Fiorenza, 2015; Fiorenza et al., 2011, 2015; Karriger et al., 2016; Krueger et al., 2017; Pérez-Pérez et al., 2003; Williams et al., 2018) and non-dietary behaviors related to the use of “teeth-as-tools” have been documented through the analysis of anterior dental wear (Estalrriich and Rosas, 2015; Krueger et al., 2017; Lozano et al., 2017; de Lumley, 1973). Analyses of occlusal microwear textures (El Zaatari et al., 2011, 2016) and macrowear (Fiorenza et al., 2011) indicate that the diet of Neandertals from cold steppe habitats falls within the range of Holocene hunter-gatherers who consumed a large amount of meat. However, the dental calculus of Spy I suggests starchy plant foods were subjected to heat treatment before being consumed, including the remains of underground storage organs and grass seeds (Henry et al., 2011). The inference that plant foods were regularly consumed by the Neandertals of Spy cave was supported by nitrogen isotope signals (Naito et al., 2016, 2018). Meanwhile aDNA evidence from dental calculus intimates that Spy II consumed more meat than plants compared to individuals from El Sidrón in which only plants were detected (Weyrich et al., 2017), and helps corroborate evidence of meat consumption previously inferred from carbon isotopes (Richards and Trinkaus, 2009), particularly in northern Europe (Bocherens et al., 2001; Wißing et al., 2016).

Carbon and nitrogen isotopes have been recovered from Spy I and II as well as five individuals from Goyet cave and these have been compared to the cave faunal remains from Spy, Goyet and Scladina Mousterian levels (MIS 3). Mammoth was an important component of the diet in every individual (Wißing et al., 2016), and the Neandertals uniformly fell within the carnivore guild with respect to carbon isotope values. Noteworthy however is that Spy I and Spy II were less enriched than the individuals from Goyet. Spy I had among the lowest contribution of mammoth meat (30%) whereas Spy II and the Goyet individuals had higher values (Wißing et al., 2016). Other resources consumed by Spy I included rhinoceros, reindeer and bovids (Bocherens et al., 2001; Wißing et al., 2016).



Fig. 1. Map of Belgium showing the approximate location of the cave where Spy I was discovered.

Fig. 1. Carte de la Belgique montrant l'emplacement approximatif de grotte où Spy I a été découvert.

While carbon isotopes and stone tools provide a signal of meat consumption, nitrogen isotopes can infer the degree to which the diet comprised plant proteins (Naito et al., 2016, 2018), which at Spy cave was apparently quite elevated. Direct evidence of underground storage organ tissue and seeds preserved in the dental calculus of Spy I contradicts a diet devoid of plants (Henry et al., 2011). These different dietary reconstructions suggest a reexamination of Spy I is indeed warranted.

1.3. Providing a context to evaluate the dental microwear texture of Spy I

Neandertals from the terminus of MIS 3 may have differed in dietary proclivities from other chronological periods and ecogeographic zones, and the cold steppe habitat coupled with extreme frigid temperatures and aridity may have limited the availability of plant resources. To further expand the reconstruction of the dietary proclivities of this late MIS 3 Neandertal adult, Spy I is compared to climate groupings that correspond to two reconstructed ecological zones. These include emergent coastal Mediterranean plains, represented by five individuals from Hortus cave, and a continental grouping typified during MIS 3 as comprising mixed conifer and deciduous forests (Fiorenza et al., 2015). This continental grouping is inclusive of La Quina 5 (southwest France), Malarnaud (French Pyrennees), Kúlna 1 and Svédúv stúl

(Moravia) as well as 19 individuals from Krapina and five individuals from Vindija (Croatia). The Mediterranean region was comparatively warmer and dryer than continental inland habitats, which experienced severe winter conditions resembling those in the northern European shrub tundra (Fiorenza et al., 2015). These are used as broad paleoenvironmental proxies to examine whether microwear texture has a relationship with habitat, which would imply that Spy I would be more similar to continental than Mediterranean zones. Ecogeography has been invoked previously to account for variation in Neandertal diets (Bar-Yosef, 2004; El Zaatari et al., 2011; Estalrriich et al., 2017; Fiorenza et al., 2011; Hardy, 2010; Krueger et al., 2017). Neandertals from Northern Europe are known for a diet heavily reliant on meat resources (El Zaatari et al., 2011; Fiorenza et al., 2011, 2015; Richards and Trinkaus, 2009; Weyrich et al., 2017; Wißing et al., 2016). Since people with a smaller proportion of plants in their diets have lower textural complexity ($Asfc$) values (e.g., Holocene pastoralists; Schmidt et al., 2016), we expect Spy I to have reduced $Asfc$ compared to Neandertals from comparatively warmer regions with a greater abundance of plant resources (e.g., El Zaatari et al., 2016). Since anisotropy ($eplSar$) separates Hortus young adults with elevated values from other ages (juvenile and 50+) (Williams et al., 2018), it is expected that the Spy I adult will exhibit high anisotropy ($eplSar$), either from the mastication of specific dietary items or lack of heterogeneity in jaw movements.

Table 1List of fossils examined ($n = 33$).**Tableau 1**Liste des fossiles examinés ($n = 33$).

Fossil	Sample	Ecogeography	Chronology
Hortus	($n = 5$)	Mediterranean	MIS 3
Krapina	($n = 19$)	Continental	MIS 5
Kůlna 1	RM ¹	Continental	MIS 3
La Quina 5	LM ₁	Continental	MIS 3
Malarnaud	RM ₁	Continental	MIS 5
Spy I	RM ²	Continental	Late MIS 3
Švédův stůl	LM ₁	Continental	MIS 3
Vindija	($n = 5$)	Continental	MIS 3

R: right; L: left.

In addition, 12 Holocene groups from Eurasia and North America (Karriger et al., 2016) inclusive of 173 individuals are included to infer the diet of Spy I using DMTA. We anticipate that the textural values of Spy I will be more similar to the published means for complexity (*Asfc*) and anisotropy (*epLsar*) for Holocene high-meat consuming hunter-gatherers and dissimilar to agriculturalists and pastoralists (Karriger et al., 2016).

2. Materials and methods

2.1. Materials

The right M² of Spy I is examined. Spy I is aged to be about 35 years with full eruption and substantial attrition of the molars, which are worn to a single functional plane (Twisselmann, 1971; Williams, 2013). The comparative sample includes Hortus IV, Hortus V, Hortus VI, Hortus VIII and Hortus XI, all of which are from Hortus cave located about 30 km from the Mediterranean coast of France and are dated to MIS 3 (Lebègue et al., 2010; de Lumley, 1972; de Lumley, 1973; de Lumley and Licht, 1972; Pillard, 1972) (Table 1). We also include La Quina 5 from Level 3 of Station Amont of La Quina cave in southwestern France, dated to 47–43 kya and falling within MIS 3 (Debénath and Jelinek, 1998; Discamps and Royer, 2017; Petite-Marie et al., 1971). An additional site considered is Malarnaud from the French Pyrenees, provisionally dated to MIS 5 (Petite-Marie et al., 1971). The Moravian Neandertal sites of Kůlna and Švédův stůl (Ochoz 1) of the Czech Republic, both dated to MIS 3 (Krueger et al., 2017) (Table 1) are included, as well as a sample of isolated molars from Krapina ($n = 19$) dated to MIS 5e (Rink et al., 1995) and Vindija ($n = 5$) from MIS 3 (Wild et al., 2001), both of which are from Croatia. The Hortus ($n = 5$), Krapina ($n = 19$) and Vindija ($n = 5$) assemblages, together with isolated sites ($n = 4$), represent much of the known temporal and ecogeographic distribution of European Neandertals (Table 1).

2.2. Molding and casting methods

A dental mold of the Spy I right M² was made with Coltène President light body dental silicone and loaned to FLW from the “Institut royal des sciences naturelles de Belgique” by PS. Additional dental molds were created using polyvinylsiloxane (Coltène-Whaledent) at the

“Centre européen de recherches préhistoriques de Tautavel” and the “Musée de l’Homme”. The resulting casts were created from epoxy resin and hardener (Buehler). Epoxy (Epo-Tek 301) dental casts of Kůlna and Švédův stůl from Erik Trinkaus were also included.

2.3. Microscopy

We studied Phase II wear facets on or adjacent to the protocone (e.g., Krueger et al., 2008). Emphasis was placed on facet 9 (Kay, 1981). We did not study Phase I facets, which bear more shear-related features. Instead, observations were restricted to the planar surfaces of Phase II facets, which indicate more of the crushing and grinding action of molars during occlusion (Kay and Hiiemae, 1974). We collected microwear data at 100× magnification using a white-light confocal profiler (Sensofar Plμ, Solaris Development Inc.) housed at the University of Indianapolis (Schmidt et al., 2019). Only surfaces devoid of irregularities from postmortem processes, such as deposition, excavation or casting, were included. Four scans contributed to a total sampling area of 276 × 204 μm which was reduced to 242 × 182 μm after they were digitally stitched together; the data collection process was standardized for all individuals. Surface morphology was visualized to validate whether the scanning process produced a surface showing dental microwear free of postmortem taphonomy. Specifically, we created 2D photosimulations and then 3D representations to search for irregularities (Fig. 2).

2.4. Texture variables

Textural properties of the enamel surface were described using two texture variables which were extracted from the point cloud using scale-sensitive fractal analysis (Scott et al., 2006). These included complexity (*Asfc*), or area-scale fractal complexity, which compares the coarseness of a surface at different scales of observation, from 7200 μm² to 0.02 μm². Complex surfaces result from the mastication of mechanically resistant food particles which tend to puncture the enamel matrix (Scott et al., 2006, 2012; Ungar et al., 2012). Tough foods are expected to require more homogeneous masticatory regimes than hard-brittle foods, and will tend to leave striated occlusal enamel surface damage which can be approximated using a measure of anisotropy (*epLsar*) or the “exact proportion of Length-scale anisotropy of relief” (Scott et al., 2006, 2012).

2.5. Comparison of complexity and anisotropy

A bivariate plot contrasts complexity (*Asfc*) and anisotropy (*epLsar*) values for Spy I, four isolated Neandertal sites and five individuals from Hortus cave coupled with a 100% convex hull demarcating the outermost values for this site. This comparison demonstrates the proximity of Spy I to the anisotropy (*epLsar*) values for young adults preserved at Hortus. The Spy I complexity (*Asfc*) value is compared to that of Neandertals from continental and Mediterranean zones, including the paleoecologically distinct phases of Hortus cave.

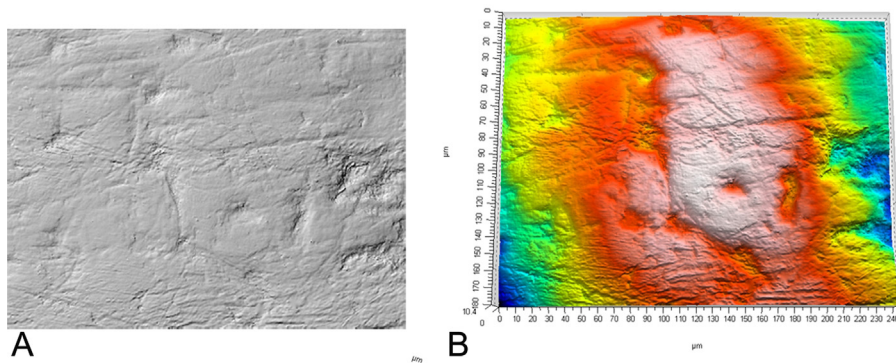


Fig. 2. Spy I occlusal molar texture shown in (a) two-dimensional photosimulations, and (b) three-dimensional enamel surface reconstructions.
Fig. 2. La texture occlusale molaire de Spy I montrée en (a) dans les photosimulations bidimensionnelles, et en (b) dans les reconstructions de surface d'émail en trois dimensions.

Spy I is additionally compared to the means and standard deviations for complexity ($Asfc$) and anisotropy ($epLsar$) of three Neandertal sites (Hortus, Krapina and Vindija) and 12 Holocene groups ($n = 173$) including Natufian hunter/gatherers from Chiu et al. (2012), North-Central Indiana Middle Woodland, Eastern Indiana Middle Woodland and Indiana Middle to Late Archaic hunter/gatherers from Frazer (2011) as well as Kentucky Archaic hunter/gatherers from Karriger et al. (2016) (Table 2). We also include agriculturalists such as Neolithic farmers from Israel (Chiu et al., 2012), Early Bronze Age England, Late Bronze Age England, Iron Age England, Iron Age Nepal (Mebrak) and Bronze and Iron Age Greece (Karriger et al., 2016). In addition, we consider the textural values for pastoralists of Mongol Xiongnu (Xiongnu Period Mongolia) and Bronze Age/Iron Age Mongolia from Schmidt et al. (2016) (Table 2). Although a variety of foraging proclivities are known from historical and archaeological hunter-gatherers, this is only a minor fraction of the variation that once existed (Kenneth, 2005). For these reasons, we acknowledge the high possibility of equifinality in all of the Holocene microwear signatures in comparison to the Middle Paleolithic samples. Microwear signals are directly linked to the mechanical properties of the foods rather than the food resources per se, and highly dependent on non-food abrasives some of which may be habitat specific. In other words, a similar microwear signature does not necessarily imply a similar diet, but it implies one with similar mechanical properties.

Since dental microwear texture data for Spy I were reported by El Zaatari et al. (2016) we compare them to the values obtained in this study. La Quina 5 is added to the comparison as both studies include this individual, albeit from molar antimeres. To provide context, Neandertal samples from open, mixed and wooded habitats are included (El Zaatari et al., 2016).

3. Results

3.1. Dental microwear textures for Spy I compared to other Neandertals

Spy I has a more elevated complexity ($Asfc$) value (2.22) than sampled from Neandertals from a Mediterranean

habitat and is closest to Kůlna 1 from the continental zone (Fig. 3). The elevated anisotropy ($epLsar$) of Spy I (0.0032) is similar to those of young adults from Hortus cave where a division by age separates young adults from juvenile and older individuals (Williams et al., 2018) (Fig. 3).

3.2. Spy I texture data compared to Neandertals and Holocene humans

When Spy I is compared to Neandertals ($n = 33$) as well as 12 Holocene groups ($n = 173$) for complexity ($Asfc$), this adult is more than one standard deviation above the mean value for the Hortus, Krapina and Vindija assemblages, and all of the Holocene humans with the exception of some of the early farmers from the Neolithic period of Israel (Fig. 4). The complexity ($Asfc$) value for Spy I is most similar to the means for prehistoric temperate hunter-gatherers of the Americas. For anisotropy ($epLsar$), Spy I falls within the Hortus, Krapina and Vindija assemblages, and it is higher than the means for prehistoric temperate hunter-gatherers of the Americas (Fig. 5). With respect to Holocene groups, Spy I is unlike the means for farmers and pastoralists with more fibrous diets (Fig. 5).

3.3. Spy I texture data compared between confocal profilers

When the textural values for Spy I are compared to those from El Zaatari et al. (2016), nearly identical positions are apparent for anisotropy (Fig. 6). For complexity, however, our Spy I value is higher. The El Zaatari et al. (2016) value hints at plant consumption and the data from our study support that interpretation. The overlapping values of the wooded and mixed Neandertal habitats are inclusive of the values for complexity obtained for Spy I. For comparison, the values for La Quina 5 are more similar for complexity than for anisotropy between the studies yet both group this specimen with open-habitat Neandertals (Fig. 6).

Table 2

Comparative Holocene sample (n = 173).

Tableau 2

Échantillon holocène comparatif (n = 173).

Sample and subsistence pattern	Culture and diet	Climate	Years BP
Early Bronze Age England farmers (n = 10) ^a	Beaker tradition, contemporaneous with Stonehenge; wheat, barely, spelt, rye, sheep, cattle and pigs with scarce evidence for the consumption of wild foods ^e	Wet-cold, temperate forest and farmland	4500–3500
Late Bronze Age England farmers (n = 11) ^a	Wheat, barely, spelt, rye, sheep, cattle and pigs, with scarce evidence for the consumption of wild foods ^e	Wet-cold, temperate forest and farmland	3500–2200
Iron Age England farmers (n = 6) ^a	Wheat, sheep, cattle and pigs with scarce evidence for the consumption of wild foods ^e	Wet-cold, temperate forest and farmland	2200–1800
Iron Age Nepal (Mebrak) farmers (n = 10) ^a	Barley, buckwheat and goats ^f	Dry-cold	2350–1300
Bronze Age Greece farmers (n = 5) ^a	Late Helladic; wheat, barley, olives, goats, sheep and cattle ^g	Dry-warm Mediterranean	1750–1250
Iron Age Greece farmers (n = 10) ^a	Protogeometric; wheat, barley, olives, goats, sheep and cattle ^g	Dry-warm Mediterranean	1250–1100
Mongol Xiongnu herders, west, north and central Mongolia (n = 29) ^a	Sheep, goats, cattle, camels, yaks, horses; traded with farmers for millet ^h	Dry-cold open habitat	3200–2300
Late Bronze/Early Iron Age herders, west, north and central Mongolia (n = 20) ^a	Sheep, goats, cattle, camels, yaks; horses traded with farmers for millet ^h	Dry-cold open habitat	2500–1850
Natufian hunter/gatherers, Israel (n = 15) ^b	Abrasive food foragers with a reliance on poorly processed, fibrous and tough foods, including acorns, pistachios, almonds, wild emmer and other cereals, seeds and gazelle ^{d,i}	Dry-warm Mediterranean	10,000
Neolithic farmers, Israel (n = 16) ^b	Wheat, barely, sheep, goats with some wild foods, including wild cereals, edible seeds, rye and pitted fruits ^{b,i}	Dry-warm Mediterranean	8000
Indiana Middle Woodland hunter/gatherers (n = 30) ^c	Hard food foragers with a mixed economy; collected nuts and seeds; hunted deer and small mammals; fished; grew <i>Chenopodium</i> , knotweed and sumpweed ^{b,d}	Wet-cold temperate	2000
Indiana Middle to Late Archaic hunter/gatherers (n = 13) ^c	Hard food foragers with a reliance on nuts and seeds, as well as deer and rabbit ^{b,d}	Wet-cold temperate	2500
Kentucky, Archaic hunter/gatherers (n = 13) ^d	Abrasive food foragers with a reliance on poorly processed, fibrous and tough foods, as well as deer and rabbit ^{d,i}	Wet-cold temperate	3000

^a Schmidt et al., 2016.^b Frazer, 2011.^c Chiu et al., 2012.^d Karriger et al., 2016.^e Fitzpatrick, 2011; Harding, 2000.^f de Gregory, 2012; Dickinson, 2006.^g Knörzer, 2000; Alt et al., 2003; Eng and Aldenderfer, 2011; Aldenderfer, 2013.^h Makarewicz, 2011; Barfield, 2001; Di Cosmo, 2002; Hanks, 2010; Machicek and Zubova, 2012; Murphy et al., 2013; Honeychurch, 2014.ⁱ Fagen, 1995.

4. Discussion

4.1. Comparison of Spy I to Hortus

With respect to the Hortus assemblage, Spy I may have consumed or processed more fibrous plants than individuals from the cold/arid paleoclimate of Sub-Phase Vb, all of whom may have had a diet richer in meat. Spy I is closer to Neandertals of the continental group than to the Mediterranean zone.

It is possible to suggest that Spy I replicates the division of diet with respect to age existing within the Hortus assemblage, in which anisotropy (*epLsar*) is low in juvenile Hortus III and older Hortus XI and highly elevated only in the four young adults from different paleoecological phases of Hortus cave (Williams et al., 2018). In a study of dental microwear texture analysis of the Neandertals from El Sidròn in northern Spain, most of the adults show elevated anisotropy (*epLsar*) whereas El Sidròn Juvenile 1 exhibits one of the lowest values of the assemblage

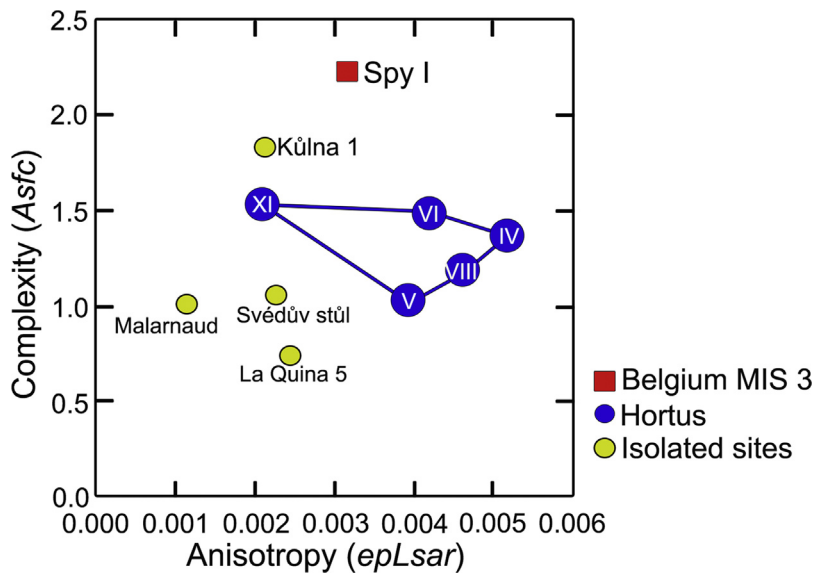


Fig. 3. Bivariate plot of complexity (*Asfc*) versus anisotropy (*epLsar*). A convex hull encompasses 100% of the Hortus assemblage.
Fig. 3. Graphique bivarié de la complexité (*Asfc*) et de l'anisotropie (*epLsar*). Une coque convexe englobe 100 % de l'assemblage de l'Hortus.

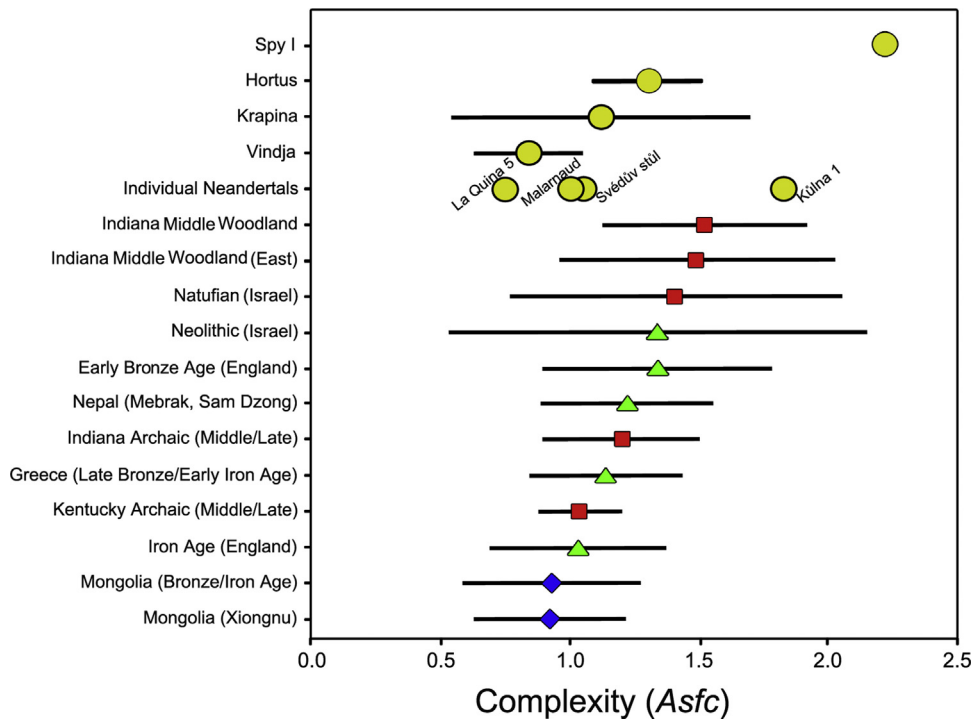


Fig. 4. Complexity (*Asfc*) for Spy I compared to other Neandertals and the textures from 12 Holocene groups. Yellow circles: Neandertals, red squares: hunter-gatherers, blue diamonds: pastoralists, green triangles: agriculturalists. Horizontal bars: 1 standard deviation.

Fig. 4. Complexité (*Asfc*) pour Spy I par rapport aux autres Néandertaliens et textures de 12 groupes holocènes. Cercles jaunes : Néandertaliens, carrés rouges : chasseurs-cueilleurs, losanges bleus : pasteurs, triangles verts : agriculteurs. Barres horizontales : 1 écart-type.

(Estalrich et al., 2017). Perhaps the lack of heterogeneous masticatory movements of the jaws in Neandertal adults is evidence of considerable effort to chew tough, fibrous foods, a pattern noted to occur as well at Krapina (Karriger et al., 2016).

4.2. Dietary reconstruction of *Spy I*

Although the open steppe was a harsh climate, isolated stands of oak and pine existed which contained a variety of plant resources perhaps exploited by *Spy I*. There

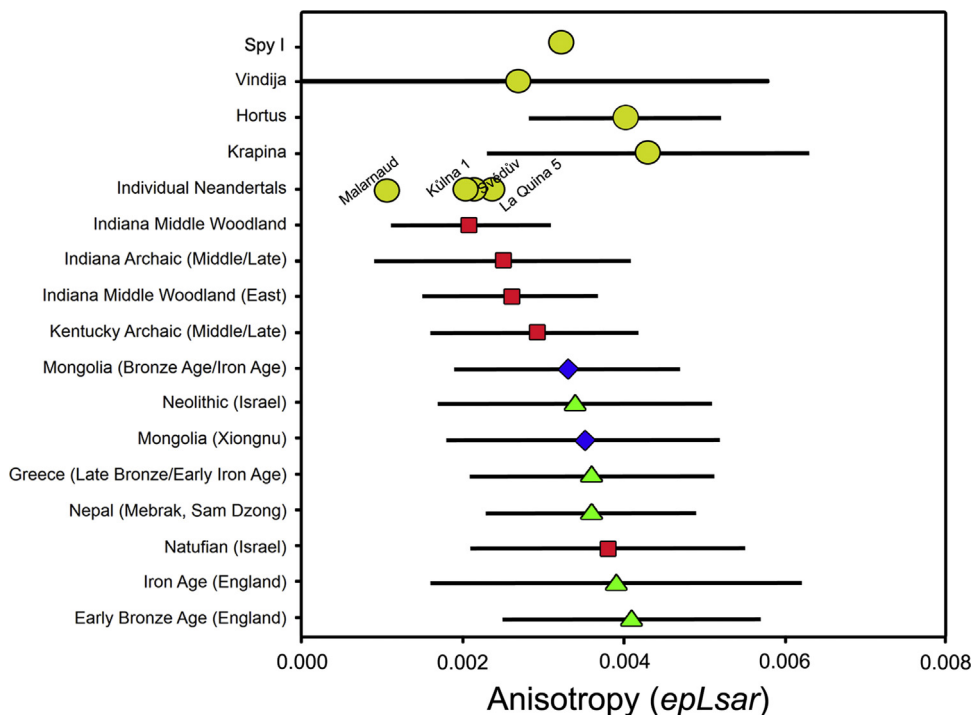


Fig. 5. Anisotropy ($epLsar$) for Spy I compared to other Neandertals and the textures from 12 Holocene groups. Yellow circles: Neandertals, red squares: hunter-gatherers, blue diamonds: pastoralists, green triangles: agriculturalists. Horizontal bars: 1 standard deviation.

Fig. 5. Anisotropie ($epLsar$) pour Spy I par rapport aux autres Néandertaliens et textures de 12 groupes holocènes. Cercles jaunes : Néandertaliens, carrés rouges : chasseurs-cueilleurs, losanges bleus : pasteurs, triangles verts : agriculteurs. Barres horizontales : 1 écart-type.

are many edible plants on steppe landscapes. For example, geophytes are common as are certain open woodland trees such as terebinth and oak (Hillman, 1996; Primavera and Fiorentino, 2013; Power and Williams, 2018). Oak acorns, hazelnut and low-lying chenopods may have been available at least seasonally on the open steppe during the late Pleistocene, allowing for a considerable amount of plant food to be incorporated into Middle Paleolithic diets (Power et al., 2018). Although Mediterranean habitats are more productive and exhibit greater tree cover, much of the biomass can be found in inedible tree trunks. In comparison, open-steppe habitats present lower productivity; however, these ecologies may exhibit a greater diversity and abundance of edible plants compared to warmer climate regimes (Power et al., 2018). Although warmer climates may have reduced levels of preservation compared to colder ones, Neandertals in both the northern and southern regions of western Eurasia appear to have utilized plant food resources in comparable frequencies (Power et al., 2018).

For example, at Spy cave, the roots of water lilies or other underground storage organs appear to have been exploited (Henry et al., 2011). Water lilies in the diet of Spy I could represent a significant part of the carbohydrates intake. This is not visible in stable isotopes given the fact that water lily roots are very poor in proteins (and DNA) and to a selective fractioning of animal proteins by human metabolism. Nevertheless, the work of Naito et al. (2016, 2018) demonstrates that the stable isotope signatures of Spy I and II are

also compatible with a protein intake of 10% of plant proteins, which means 80% of the diet. Furthermore, starchy grains in Neandertal dental calculus have been discovered as early as MIS 7/8 and are increasingly prevalent after 50,000 years BP, including those from Spy cave, suggesting a regular dietary intake of plant foods (Hardy and Moncel, 2011; Hardy et al., 2012). Neandertal consumption of these starchy plant foods does not contradict the results of isotope analyses, because nitrogen isotopes record only the consumption of meat and protein-rich plant foods (Power et al., 2018).

A study of microwear by Garcia Martin (2000) on the vestibular or buccal molar surface (method of Molleson) using scanning electron microscopy also found considerable evidence of plant food consumption, grouping Spy II with the Neolithic inhabitants of Belgium which in addition to agricultural products included substantial hunted and gathered resources in the diet (Semal et al., 1999). Spy I differed from the Belgian Neolithic cave burials and had a greater resemblance to medieval monastic cemetery populations such as Coxyde (Garcia Martin, 2000). Our Spy microwear signature is similar to that of El Zaatari et al. (2016), particularly in terms of anisotropy. The values from each study are almost identical. Our complexity value is higher than what El Zaatari et al. (2016) report, but this difference is difficult to explain. The studies used different profilers and interprofiler differences have been reported (Arman et al., 2016), but the system at the University of Indianapolis has been calibrated to the profiler used

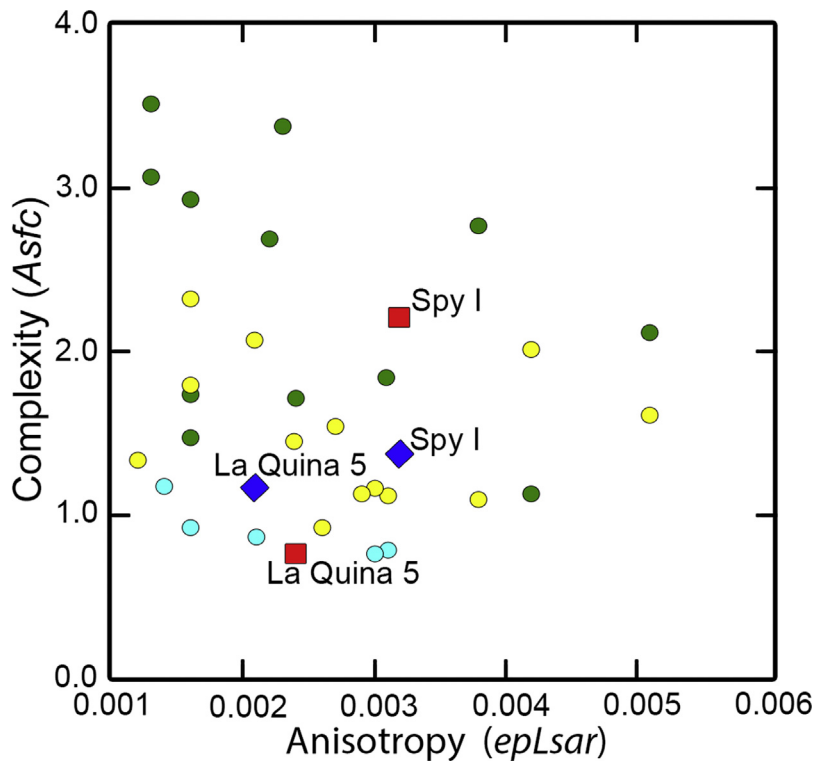


Fig. 6. Comparison of Spy I and La Quina 5 in this study (red squares) and in El Zaatari et al. (2016) (blue diamonds) with Neanderthal samples from open (turquoise circles), mixed (yellow circles) and woodland (green circles) habitats (El Zaatari et al., 2016).

Fig. 6. Comparaison de Spy I et La Quina 5 dans cette étude (carrés rouges) et dans El Zaatari et al. (2016) (losanges bleus) avec des échantillons de Néandertal provenant d'habitats ouverts (cercles turquoise), mixtes (cercles jaunes) et boisés (cercles verts) (El Zaatari et al., 2016).

by El Zaatari at the University of Arkansas (Schmidt et al., 2016). In any event, the two studies are likely telling similar stories in that both values indicate some level of dietary hardness and neither clusters with, for example, soft food eating groups like the Holocene pastoralists. This confirmation of microwear signatures is important because it shows that different researchers can make similar determinations, but they can also detect subtle nuances that may open up opportunities to explore new interpretations of diet.

4.3. Explaining the elevated complexity in Spy I

The elevated complexity ($Asfc$) of Spy I indicates the consumption of hard particles such as nuts, seeds, shells and exogenous grit given the association between this textural property and hard plant particle consumption (Calandra et al., 2012; DeSantis et al., 2013; Schmidt et al., 2016, 2019; Scott et al., 2005, 2006, 2012). Since meat is a soft food, it is unlikely to damage the surface enamel such that pastoral Holocene populations exhibit much lower values (Schmidt et al., 2016). The elevated complexity ($Asfc$) of Spy I could derive from the consumption of the hard parts of seasonally available plants, such as seeds, or possibly from underground storage organs (Hardy, 2010), which may have contributed inadvertent grit to the occlusal surface during mastication. Since virtually no food processing technology has been recovered from the site, it is likely that the natural hardness of the foods was not

mechanically reduced prior to consumption. A combination of foods, some of which were rather hard and brittle, and other resources that the individual could acquire likely led to the relatively high degree complexity ($Asfc$) of the enamel surface.

Although the aDNA analysis of dental calculus by Weyrich et al. (2017) suggest Spy II had a meat-based diet, the earlier analysis of plant microfossils contained in the Spy I and II calculus indicates the consumption of starch-rich plants and grass seeds (Henry et al., 2011). Such a finding is consistent with a dental microwear texture analysis of Spy I indicative of the mastication of plant materials on a level similar to that of the Chumash (El Zaatari, 2007, cf. El Zaatari et al., 2011), a mid-Holocene archaeological population from Santa Cruz Island, California who were hunter/gatherer/fishers, exploiting clams, abalone, mussels, fish, and shark as well as migratory birds, otter, sea mammals, duck, quail, bear, deer, acorns, herbs, seeds, nuts, bark, berries, leaves and bulbs (Colten, 1996; Kenneth, 2005; Timbrook, 1986, 1993). The Spy I Neanderthal could have consumed hard seeds, underground storage organs and other plant parts or grit resulting in an elevated complexity ($Asfc$) value. Yet hard foods can mask meat consumption. Given that the Spy I microwear texture signature indicate both hard and fibrous foods, it is likely that most plant foods were poorly processed if at all, and could have been consumed in their natural state.

Thus, the microwear data from the current study contributes to an important multi-faceted approach that adds to existing studies of the Spy I teeth; specifically it has both verified the anisotropy and clarified the complexity values provided in previous works.

5. Conclusion

To the degree to which the results were unaffected by a limited sample size, there is strong evidence that the enamel textural complexity (*Asfc*) of Spy I is most similar to the means of temperate hunter-gatherers of the Americas who consumed a hard diet comprising seeds, nuts and unprocessed foods. Spy I may have consumed more seasonal plant-based resources than other Neanderthals who appear to have had meat-rich diets. Spy I may have lived during a period of less extreme temperatures during the periodic glaciations of MIS 3 (Semal et al., 1999, 2011, 2013), and a greater number and variety of plant foods may have been available compared to the other Neanderthals such as those preserved at Hortus from Sub-Phase Vb (Lebègue, 2012; Lebègue et al., 2010; de Lumley, 1973; Williams et al., 2018). Plant particles preserved as microfossils in the dental calculus of Spy I also attest to the consumption of plants, such as starches from underground storage organs including water lilies, and to a lesser extent on grass seeds from Andropogoneae, the subfamily including sorghum (Henry et al., 2011). Terrestrial plant resources would have contributed grit to the diet as would the hard seed coats of grasses. Other foods with similar mechanical properties may have also damaged the occlusal enamel surface. Although plants were an important diet resource for Spy I, plants did not replace meat. It is likely that the plant signature swamped the one for meat. We suspect both were vital.

Concerning anisotropy (*epLsar*), Spy I is again just above the means of temperate hunter-gatherers of the Americas. With respect to other Middle Paleolithic sites, Spy I adds further evidence for the division of diet by age for anisotropy (*epLsar*) observed at Hortus cave and possibly Krapina suggesting a common Neanderthal adult pattern of heavy unidirectional masticatory behavior to process tough, fibrous foods or other resources, such as grasses used for bedding (Cabanès et al., 2010). Late MIS 3 Neanderthals of the Meuse River Basin of Belgium such as Spy I, like their counterparts at Hortus and Krapina, may have relied on a division of dietary or paramasticatory behavior by age as a means of survival in the cold, arid and often inhospitable frontier of northern Europe.

Uncited references

Di Modica, 2011; El Zaatari, 2010; Pérez-Pérez et al., 2017; Pirson et al., 2014; Ungar, 2015.

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