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Dental microwear texture analysis of Neandertals from Hortus cave, France

Analyse de la texture des de la micro-usure dentaire chez les Néandertaliens de la grotte de l'Hortus, France

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ABSTRACT

The dental microwear textures of six individuals from Hortus cave, France are compared to Neandertals from different ecological zones and time periods. Molar Phase II facets were scanned using white-light confocal microscopy and scale sensitive fractal analysis yielded enamel surface textural characteristics. The juvenile Hortus III and the older adult Hortus XI exhibit relatively low anisotropy (*epLsar*) and textural fill volume (*Tfv*) and are distinct from young adults with higher values. These differences may be related to age, such that only young adults were engaged in the mastication of tough, fibrous vegetation, whereas Hortus XI (50+ years) and Hortus III (6.5–7.9 years) did not. Sub-Phase Vb Hortus individuals exhibit reduced dietary hardness (*Asfc*) suggesting a greater reliance on soft foods, like meat. Differences between individuals from Hortus cave correspond to both sub-phase variation in climate and intrinsic lifeways.

RÉSUMÉ

La texture des microtraces d'usure dentaire de six individus provenant de la grotte de l'Hortus (France) est comparée à celles de Néandertaliens provenant de différentes zones écologiques et ayant vécu à différentes périodes chronologiques. Dans ce cadre, les facettes des molaires de la phase II ont été scannées au moyen d'un microscope confocal à lumière blanche, et une analyse fractale sensible à l'échelle a fourni les caractéristiques texturales de surface de l'émail. Le spécimen juvénile Hortus III et l'adulte

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Spy 1
Svédův stůl
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le plus âgé Hortus XI présentent une anisotropie (*epLsar*) et un volume de remplissage textural (*Tfv*) relativement faibles, et sont distincts de ceux des jeunes adultes ayant des valeurs plus élevées. Ces différences peuvent être liées à l'âge : c'est ainsi que les jeunes adultes se sont engagés dans la mastication de la végétation fibreuse dure, au contraire d'Hortus XI (50 ans et plus) et d'Hortus III (entre 6,5 et 7,9 ans). Les individus de la sous-phase Vb de l'Hortus témoignent d'une consommation d'aliments durs réduite (*Asfc*), suggérant une plus grande dépendance vis-à-vis des aliments mous, comme la viande. Les différences entre les individus de la grotte de l'Hortus sont liées à la variation de la sous-phase du point de vue du climat et des modes de vie intrinsèques.

1. Introduction

Hortus cave is positioned between the piedmont region south of the Languedoc Mountains of the Massif Central and the Mediterranean Sea, about 30 km northwest of Montpellier, France (Lumley, 1972, 1973). Although the cave was known for generations, it was first excavated in 1906–1908. Between 1949 and 1954, late Bronze Age deposits were identified. Five large-scale excavations were conducted between 1960 and 1964 under the direction of Henry de Lumley. During this interval, the remains of between 20 to 33 Neandertals, as well as Mousterian tool assemblages, Pleistocene fauna and palynological remains were recovered.

The dietary proclivities of these Neandertals have been previously reconstructed using faunal remains (Pillard, 1972) and inferred from the tools used to process them (Lebègue, 2012; Lebègue et al., 2010; Lumley and Licht, 1972). Additional research has documented enamel chipping and lithic-induced cultural striations on the anterior teeth of the Neandertals from Hortus that indicate extensive participation in non-masticatory (e.g., "stuff-and-cut") behaviors (Estalrrich and Rosas, 2015; Lumley, 1973). However, this is the first study aimed at reconstructing the dietary signatures of the Neandertals from several phases and sub-phases of the site using dental microwear texture analysis (DMTA). The DMTA dietary signatures of the inhabitants of Hortus cave are inferred through comparisons with a geographically extensive sample of Middle Paleolithic Neandertals and Holocene humans.

1.1. Cave stratigraphy and anthropogenic activity

The earliest evidence of human modification of the environment at Hortus cave exists in Phase I and II, which is subsequent to Marine Isotope Stage (MIS) 5e. The stalagmitic floor dates from MIS 5e, but not the deposition of the cavity. All layers, from Phase I to Sub-Phase Vc, include Mousterian and Mousterian-like artifacts (Lumley, 1972, 1973). By Phase III and a part of Sub-Phase IVa, human modification of the cave would become more regular (Lebègue et al., 2010) and is characterized by a typical Mousterian industry (Lebègue, 2012; Lumley, 1973; Lumley and Litch, 1972). These temporary hunting camps were likely to have been of a short duration and indicate a near exclusive focus on ibex hunting and processing by hunters rather than the entire social group (Lebègue et al., 2010; Pillard, 1972). This type of occupation was eventually replaced with a seasonal exploitation of the site whereby a greater emphasis was placed on the movement of the group rather than just the hunters (Lebègue et al., 2010), coinciding with an environmental shift from more humid to predominantly dry vegetation (Lumley, 1972, 1973, 1976). Sub-Phase IVb and Phase V show evidence of a diversity of activities as opposed to solely the butchering of animals. These include hearths that have been repeatedly used (Lebègue et al., 2010). Sub-Phase IVb and Phase V represent temporary camps that were economically self-sufficient and occurred during a single season. The presence of children and adults of different ages suggests a small social unit or "micro-band" during these phases (Lebègue et al., 2010).

Whereas Mousterian tools are found throughout the MIS 3 deposits, Neandertal remains are only found in the more recent levels, including Sub-Phase IVa, IVb, Va, Vb and Vc. Besides two neonatal parietal fragments, all the dental remains were found *in situ* within the phases. One exception is Hortus VI, a left mandibular third molar (M_3), which lacks provenience (Lumley, 1973; Tables 2–3). Hortus VI was discovered in 1964, which postdates the excavation of the other remains recovered between 1960 and 1963 (Lumley, 1972, 1973).

The climate of Sub-Phase IVb was cold and dry while Sub-Phase Va and Sub-Phase Vb experienced extreme cold and aridity (Lumley, 1973). The phases also preserve slightly different tool types, which has implications for the foods consumed (Table 1). Sub-Phase IVb is associated with a typical Mousterian assemblage whereas, Sub-Phase Va and Vb are characterized by Mousterian tools infused with denticulates suggesting smaller food items may have been processed (Lumley, 1973). When the landscape was increasingly opened by continued drying during MIS 3, groups began to settle in the vicinity of Hortus cave for a longer duration and subsequently carried out a more diversified set of activities related to their subsistence strategies and diet.

1.2. Paleoecological reconstruction

The five large stratigraphic layers (or phases) at Hortus cave record cycles of cold, alternating between more and less intense, combined with variation in levels of humidity and increasingly arid conditions. The major phases are interspersed between short interphases that exhibit a greater resemblance to temperate climates (Table 1). Paleosols evince a paleoclimate that was relatively cold

Table 1
Climate indicators and cultural remains for Phase I to V of Hortus cave.
Tableau 1
Indicateurs climatiques et vestiges culturels pour la phase I à V de la grotte de l'Hortus.

Phase	Sub-Phase	Climate	Pollen	Fauna	Tools/fossils examined[a]
Phase V	Sub-Phase Vc	Cold–dry/Very cold–dry	Sage Thistle Flowering plants (Anthemidae)	*Felis* *Ursus* *Cervus* *Capreolus* *Capra* *Rangifer* *Equus caballes* *Oryctolagus* *Eliomys* *Microtus*	Typical Mousterian (*n* = 309)
	Sub-Interphase Vb-Vc	Cold–dry/ Extreme cold–dry	Small forests of pine and oak		
	Sub-Phase Vb	Very cold/ Extreme cold–dry	Thistle Flowering plants (Anthemidae) Sage	*Felis* *Ursus* *Cervus* *Capra* *Bos/Bison* *Equus caballes* *Rhinoceros* *Oryctolagus* *Apodemus* *Eliomys* *Glis* *Crocidura* *Microtus*	Typical Mousterian supplemented with denticulates (n = 200) Hortus III, Hortus V, Hortus VIII
	Sub-Interphase Va-Vb	Very cold–wet	Small forests of conifers		
	Sub-Phase Va	Very cold–dry	Flowering plants/shrubs (Cichorieae/Anthemidae) Thistles Sagebrush/wormwood	*Ursus* *Cervus* *Capra* *Equus caballes* *Oryctolagus* *Apodemus* *Eliomys* *Glis*	Typical Mousterian/ Typical Mousterian supplemented with denticulates (n = 252) Hortus XI
	Interphase IV–V	Temperate–dry	Return of trees, scattered pines, conifers		
Phase IV	Sub-Phase IVb	Less cold/very cold/cold–dry	Grasses, flowering plants/shrubs (Cichorieae) Sagebrush/wormwood	*Equus* sp. *Canis* *Cervus* *Capra* *Bos/Bison* *Oryctolagus* *Apodemus* *Eliomys* *Glis* *Pitymys*	Typical Mousterian (*n* = 226) Hortus IV

Table 1 (*Continued*)

Phase	Sub-Phase	Climate	Pollen	Fauna	Tools/fossils examined[a]
	Sub-Interphase IVa–IVb		Disappearance of trees		
	Sub-Phase IVa	Cold–wet	Dominance of oaks, pines; extension of conifers and oak	*Ursus*	Typical Mousterian supplemented with denticulates
			Presence of linden trees	*Cervus*	(*n* = 83)
			Dominance of pine	*Capra* *Bos/Bison* *E. hydruntinus* *Oryctolagus* *Apodemus* *Glis* *Clethrionomys* *Crocidura*	
	Interphase III–IV	Temperate-wet	Pine forests and fewer oaks		
Phase III		Cold–wet/	Appearance of linden trees; dominance of pine and oak; birch is rare; dominance of pine and oak; decline of grasses	*Felis*	Typical Mousterian
		Very cold–dry/ Cold–wet		*Ursus* *Capra* *Oryctolagus* *Apodemus* *Eliomys* *Glis*	(*n* = 23)
	Inter-Phase II–III	Temperate-wet	Pine forest		
Phase II		Cold–wet/	Disappearance of birch		Near-absence of Mousterian and Mousterian-like artifacts
		Cold–dry	Abundance of pine and grasses; presence of birch		
	Interphase I–II	Temperate-wet	Oaks without birch		
Phase I		Cold–very wet	Maximum of birch; birch and grasses; few pine		Near-absence of Mousterian and Mousterian-like artifacts

[a] Excludes Hortus VI.

corresponding to the ecological variation noted to have occurred in MIS 3 (Lumley, 1972, 1973).

1.2.1. *Large fauna*

Many animal species are found throughout Phases III to V, although in varying abundance (Table 1) (Lumley, 1972, 1973). Carnivores include wolves (*Canis lupus*) which are found in Sub-Phase Vb. Large cats including *Felis leo pardus* and *Felis panthera* are found in varying amounts in Sub-Phase Vc and Vb, as well as in Phase III. Cave bears (*Ursus spelaeus*) are found in large numbers in Sub-Phase Vc, Vb, Va and in smaller quantities in Sub-Phase IVa and Phase III (Pillard, 1972).

Various ungulates are present including red deer (*Cervus elaphus*) and caribou (*Rangifer tarandus*) which are found in Sub-Phase IVa and IVb as well as Sub-Phase Vb and Vc; the western roe deer (*Capreolus capreolus*) is found in small quantities only in Sub-Phase Vc; ibex (*Capra ibex*) is found in large quantities from Phase III to the terminus of Sub-Phase Vc, particularly in Sub-Phase Vb and Phase III; and oxen/bison (*Bos/Bison* sp.) are found in somewhat larger quantities in Sub-Phase Vb compared to Sub-Phase IVa and IVb (Lumley, 1972, 1973; Pillard, 1972).

Equids including horses (*Equus caballes*) are found in greater quantities in Sub-Phase Va and Vb and are fewer in Sub-Phase IVb and Vc; however, the European donkey, *Equus* (*Asinus*) *hydruntinus*, is found in Sub-Phase IVa, signally the increasing dryness of Phase IV and V (Table 1). Rhinoceros (*Dicerorhinus* sp.) is found only in Sub-Phase Vb (Lumley, 1972, 1973; Pillard, 1972).

1.2.2. *Small fauna and other environmental proxies*

Numerous rodent and insectivore taxa are found throughout the sequence containing evidence of human activity, and signal the environmental conditions in greater detail than the larger game animals brought to the cave. The presence of forests and some prairies in Phase III is indicated by field mice (*Apodemus sylvaticus*) and dormouse (*Eliomys quercinus*, *Glis glis*). Larger forest coverage of the area in Sub-Phase IVa is signaled by the presence of red-backed voles (*Clethrionomys glareolus*) along with *Apodemus sylvaticus*, *Glis* and wood shrews (*Crocidura leocoden*) that inhabit disturbed forests (Lumley, 1972, 1973; Pillard, 1972). However, forests continue to dominate in Sub-Phase IVb with the replacement of *Clethrionomys glareolus* with the pine vole (*Pitymys duodecimcostatus*) and the presence of *Eliomys sylvaticus*, *Glis*, *Apodemus sylvaticus* and *Crocidura suaveolens* (Table 1). Sub-Phase Va and Vb feature smaller clusters of forests indicated by the absence of voles and wood shrews, the dominance of *Eliomys sylvaticus* and *Glis* and the relative decline of *Apodemus sylvaticus*, while the presence of prairie moles corroborates the increasing cold and aridity through the middle of Sub-Phase Vc (Lumley, 1972, 1973; Pillard, 1972). Sub-Phase Vb witnessed the arrival of common voles (*Microtus arvalis*) and hedgehogs and the persistence of *Crocidura suaveolens* which thrives in disturbed habitats (Table 1). Rabbits (*Oryctolagus cuniculus*) are found throughout the human sequence in relatively large numbers, from Phase III to Sub-Phase Vc (Lumley, 1972, 1973; Pillard, 1972). Amphibians and reptiles are represented sporadically throughout the anthropogenic phases while non-aquatic snails, primarily *Chondrina similis*, are found throughout the sequence (Table 1).

1.2.3. Increasing cold and aridity

The more forested conditions of Phase III and IV in comparison to Phase V is supported by the increasing decline of chiropterans, which exhibit the greatest degree of speciation toward the terminus of Phase III but continue to be numerous in Phase IV. Phase V in contrast exhibits a much smaller number of bat species (Lumley, 1972, 1973; Pillard, 1972). Numerous bird species preserved in the deposits mimic to greater or lesser degrees the prevalence of bats.

The arrival of *Equus caballus* at the beginning of Sub-Phase IVb signals an increasing aridity of the climate at interphase IVa-IVb, corresponding to the stratigraphic and sediment analysis and palynology (Lumley, 1972, 1973; Pillard, 1972). The cold conditions of the anthropogenic sequence are corroborated by the abundance of the large sub-species of the European rabbit (*Oryctolagus cuniculus cuniculus*), which today is found far to the north (Pillard, 1972). The rodents and insectivores indicate an environment of forests and grasslands existing in a cold climate albeit of a Mediterranean character (Lumley, 1972, 1973; Pillard, 1972).

These environmental proxies and remains of hunted animals provide evidence of an increasingly cold and arid habitat experienced by these Neandertals. Throughout much of MIS 3, the coastal region of Mediterranean France west of the Rhone valley has been reconstructed as comprising emergent coastal planes juxtaposed with forests of mixed coniferous and deciduous trees (Fiorenza et al., 2015). The MIS 3 climate of Hortus approximated much of the Mediterranean basin including the Levant and was relatively cold and dry compared to the recent past (Fiorenza et al., 2015). The Mediterranean basin was warmer than northwestern and central Europe during MIS 3 (van Andel, 2002). Northern Hemispheric MIS 3 stadials ranged from around −9.3° degrees C in the winter months to approximately 17.3 °C in the summers (Van Meerbeeck et al., 2009). The colder temperatures corresponded to drier climates with a sharp decrease in precipitation, particularly in the winter months, resulting in shifts in vegetation and fauna (Álvarez-Lao and Méndez, 2016; Van Meerbeeck et al., 2011). The relatively cold and arid climate conditions of MIS 3 likely affected the dietary behavior of the individuals preserved at Hortus cave.

1.3. Dental microwear texture analysis

Dental Microwear Texture Analysis (DMTA) has been previously utilized to reconstruct fossil hominin diets (Scott et al., 2005; Ungar et al., 2012), including those of Neandertals (El Zaatari et al., 2011, 2016; Estalrrich et al., 2017; Karriger et al., 2016; Krueger et al., 2017). DMTA captures three-dimensional textures on worn enamel surfaces that correspond to the mechanical properties of the foods consumed (Schmidt et al., 2016; Scott et al., 2005, 2006, 2012; Ungar et al., 2012). Antemortem dental microwear reveals the foods masticated in the last few days or weeks of an individual's life (Ungar, 2015). As such, short-term dietary changes and seasonality can be inferred from DMTA. The most profound differences in Neandertal DMTA signatures exist between individuals from paleoenvironments that reflect open habitats and those from sites that suggest greater vegetation coverage or wooded settings – the former characterized by high meat consumption and the latter emphasizing mixed meat and vegetable foods (El Zaatari et al., 2011, 2016; Estalrrich et al., 2017). A similar, habitat-driven difference in anterior tooth-use has also been documented among Neandertals using DMTA (Krueger et al., 2017). Krapina was shown to differ from Vindija in its elevated anisotropy, or patterning, suggesting substantial amounts of tough vegetation, such as plant fibers or underground storage organs, may have been consumed (Karriger et al., 2016). Additional research on Neandertal buccal microwear (Pérez-Pérez et al., 2003, 2017; Pinilla et al., 2011) and occlusal macrowear (Fiorenza et al., 2011; Fiorenza, 2015; Pinilla et al., 2017) also suggests extensive variability in Neandertal diets with respect to chronology, paleoenvironment, climate and cultural factors.

Texture variables from DMTA capture different aspects of dietary diversity. For example, herders, who consume large amounts of meat, exhibit lower values for dental microwear textures than do agriculturalists (Schmidt et al., 2016). Meanwhile, plant foods, or food processing strategies, can introduce grit and other hard particles such as phytoliths and seed shells that tend to inflict damage to the enamel surface resulting in higher textural values (Calandra et al., 2012; DeSantis et al., 2013; Karriger et al., 2016). Because different profilers, file parameters and generations of software compromise the complementarity between machines (Arman et al., 2016), all the textural data presented here are from a single profiler at the University of Indianapolis.

1.4. Hypotheses

If the individuals preserved at Sub-Phase IVb and Phase V of Hortus consumed similar seasonally based resources, they should have a uniform dietary profile unless the increasingly cold and dry conditions influenced the availability of plant resources. Based solely on stratigraphy, it would be expected that individuals excavated from Sub-Phase Vb, Hortus III, Hortus V and Hortus VIII, should cluster in dental microwear textures. Hortus XI from Sub-Phase Va should be secondarily joined to the individuals in Sub-Phase Vb. It may be expected that Hortus IV, from Sub-Phase IVb which is older, should differ from the individuals from Sub-Phase V which was colder and more arid. A recent analysis of microwear textures from the El Sidrón Neandertals contextualized sample variation with respect to age, sex and maternal lineage, and found key differences in anisotropy (*epLsar*) by sex and some idiosyncratic variation in scale of maximum complexity (*Smc*) (Estalrrich et al., 2017). The extensive life-stage variation among the Hortus Neandertals provides an impetus for exploring microwear textures with respect to age as well as chronology.

It is expected that the six individuals from Hortus will have a greater resemblance to one another than to Neandertals from a diverse number of ecogeographic regions and temporal horizons, from MIS 7 to MIS 3. Given prior evidence of the role of ecogeography in explaining Neandertal diets (El Zaatari et al., 2011), there may be a difference between Neandertals from the circum-Mediterranean and those from farther north. To address this question, the Hortus assemblage is compared to Neandertals from the circum-Mediterranean sites of Kebara 2 and Tabūn Series III from northern Israel and as well as a wide range of continental sites including those in central Europe (Kůlna and Švédův stůl), the French Pyrenees (Montmaurin and Malarnaud), Southwest France (La Quina 5) and the Meuse River Basin of Belgium (Spy 1). It is expected that Neandertals, known for their heavy meat consumption (Richards and Trinkaus, 2009), should have lower textural values in colder, inland habitats with little forest resources than those in circum-Mediterranean ecozones (El Zaatari et al., 2011; Fiorenza et al., 2011, 2015). To reconstruct the diet of the Hortus assemblage, they are compared to the published mean values for complexity and anisotropy for twelve Holocene societies (Karriger et al., 2016).

2. Materials and methods

2.1. Materials

The permanent and deciduous molars in this study included Hortus III, Hortus V and Hortus VIII from Sub-Phase Vb; Hortus XI from Sub-Phase Va; Hortus IV from Sub-Phase IVb; and Hortus VI which is unassociated with respect to phase (Lumley, 1973) (Table 2).

Table 2
List of fossil molars from Hortus cave included in this study.
Tableau 2
Liste des molaires fossiles provenant de la grotte de l'Hortus analysées dans cette étude.

Fossil	Molar[a]	Dental age	Sub–Phase
Hortus III (826)	Rdm^2	Juvenile (6.5–7.9 years)[b]	Vb
Hortus IV (1436)	RM_1	Subadult/Adult (17–30 years)[c]	IVb
Hortus V (693)	LM_2	Adult (18–25 years)[c]	Vb
Hortus VI (13)	LM_3	Adult (22–30 years)[c]	–
Hortus VIII (375)	RM^1	Adult (26–34 years)[c]	Vb
Hortus XI (635)	RM^3	Adult (50+ years)[c]	Va

[a] R: right; L: left.

[b] Ramirez Rozzi (2005) estimated an age of 6.5–7.9 years for Hortus II/III on the basis of perikymata, revising the estimate of ~9 years provided by de Lumley (1973). Although some researchers suggest that Neandertals developed at a much faster rate than modern humans (e.g., Smith et al., 2014), others disagree (Rosas et al., 2017; Shackelford et al., 2012) given the extensive idiosyncratic variation in late Pleistocene and Holocene human dental development.

[c] Lumley (1973).

Table 3
List of Neandertal fossil molars utilized to contextualize the Hortus assemblage.
Tableau 3
Liste des molaires fossiles néandertaliennes utilisées afin de contextualiser l'assemblage de l'Hortus.

Fossil	Molar[a]	Dental age	Ecogeography	Chronology
Kebara 2	RM_2	Adult	Mediterranean	MIS 4
Kůlna 1	RM^1	Juvenile	Continental	MIS 3
La Quina 5	LM_1	Adult	Continental	MIS 3
Malarnaud	RM_1	Subadult	Continental	MIS 5
Montmaurin	RM_1	Young adult	Continental	MIS 7
Spy 1	RM^2	Adult	Continental	MIS 3
Tabūn Series III	LM_1	Adult	Mediterranean	MIS 5
Švédův stůl	LM_1	Adult	Continental	MIS 3

[a] R: right; L: left.

The comparative sample was chosen to provide climatic and temporal extremes of western Eurasia from MIS 7 to MIS 3, and includes the molars of Kebara 2, dated to approximately 62 kyr BP (MIS 4) and Tabūn Series III from MIS 5, both from northern Israel (Grün and Stringer, 2000; Krueger et al., 2017); those of Kůlna and Švédův stůl (Ochoz 1) of the Moravian Mountains of the Czech Republic, both of which are likely to be from MIS 3 (Krueger et al., 2017; Table 3); and Spy 1 from the Meuse River Basin of Belgium, dated to near the terminus of MIS 3 at 36 kyr BP (Semal et al., 2009). The comparative sample also includes Neandertals somewhat closer to Hortus cave, including La Quina 5 from Level 3 of La Quina cave in Charente of Southwest France, discovered with middle Mousterian tools, and dated to MIS 3 at circa 43–47 kyr BP (Discamps and Royer, 2017), and the French Pyrenees sites of Malarnaud dated to MIS 5 (Petite-Marie et al., 1971) and Montmaurin, discovered in La Niche, level C3, which has been dated to MIS 7 (Crégut-Bonnoure et al., 2010) (Table 3). Although the comparative sample is limited (n = 8), the isolated fossil sites include much of the chronological and geographic range of Neandertals from western Eurasia.

2.2. Molding and casting methods

Dental molds were created at the Centre européen de recherches préhistoriques de Tautavel and the Musée de l'Homme by FLW, using polyvinylsiloxane (Colètene-Whaledent). Roc de Marsal from the collections of the Musée national de préhistoire, Les Eyzies, was also molded, but postmortem taphonomic processes led to the exclusion of this fossil from the study. Dental molds of Spy 1 were loaned to FLW from the Institut royal des sciences naturelles de Belgique by Patrick Semal. Dental casts from the molds were created from centrifuged epoxy resin and hardener (Buehler) at Georgia State University and allowed to air-dry for 24 hours before extraction. Additional dental casts (Kebara 2, Tabūn Series III, Kůlna and Švédův stůl) were provided by Erik Trinkaus.

2.3. Data capture

The dental casts were scanned at the University of Indianapolis using the "Indy" machine, a white-light confocal profiler (Sensofar Plμ) at 100 × magnification (Solarius Development Inc.). Scanning occurred on the enamel surface of the protocone of the maxillary molars and on the protoconid of the mandibular molars on phase II facets, which have been shown using DMTA to be more effective than phase I facets in distinguishing known dietary proclivities (Krueger et al., 2008). We focused on Facet 9 unless it was unsuitable for study. Then, we looked for Phase II facets adjacent to Facet 9. Only surfaces that were free of irregularities originating from fossilization, preparation or casting were considered. For each specimen, four scans were captured from a 138 × 102 μm viewing field. The total sampled area of 276 × 204 μm was condensed to a study area of 242 × 182 μm once the scans were stitched together using an automated process to form a single point cloud for each individual. To observe surface morphology, two- and three-dimensional surface representations were created (Figs. 1 and 2).

2.4. Textural variables

Once the scans were leveled within the program SolarMap Universal, the point clouds were analyzed using scale-sensitive fractal analysis (Schmidt et al., 2016; Scott et al., 2006), which yielded four variables that describe the textural properties of the enamel surface. To consider roughness and relative areas at different scales of observation, an area-scale fractal complexity (*Asfc*) algorithm was employed which compares surface texture at 7200 μm^2 to 0.02 μm^2. The mastication of hard and brittle foods will generate higher complexity than the consumption of tough, fibrous foods (Schmidt et al., 2016; Scott et al., 2006, 2012; Ungar et al., 2012). Scale of maximum complexity (*Smc*) measures aspects of enamel surface deformation that are not necessarily captured by complexity (*Asfc*), separating hard vs. hard-brittle food consumption (Scott et al., 2006).

Anisotropy (*epLsar*) or the "exact proportion of Length-scale anisotropy of relief" serves as a proxy for the degree to which foods are dragged along the occlusal surface which creates a concentrated patterning of enamel surface texture (Scott et al., 2006, 2012). Surfaces characterized by numerous parallel scratches are expected to yield high values for anisotropy.

Textural fill volume (*Tfv*) compares the volume of the scanned surface using square cuboids with different lengths (10 and 2 μm) to estimate the degree to which damage to the enamel surface is the result of dental microwear as compared to facet curvature (Scott et al., 2006). High textural fill volume characterizes hard-object consumers (Scott et al., 2012) and may reflect the consumption of mechanically challenging particles of different sizes (El Zaatari and Hublin, 2014).

Texture variables are plotted against one another using a convex hull around individuals from Hortus and the values for the eight Neandertals from isolated sites. A

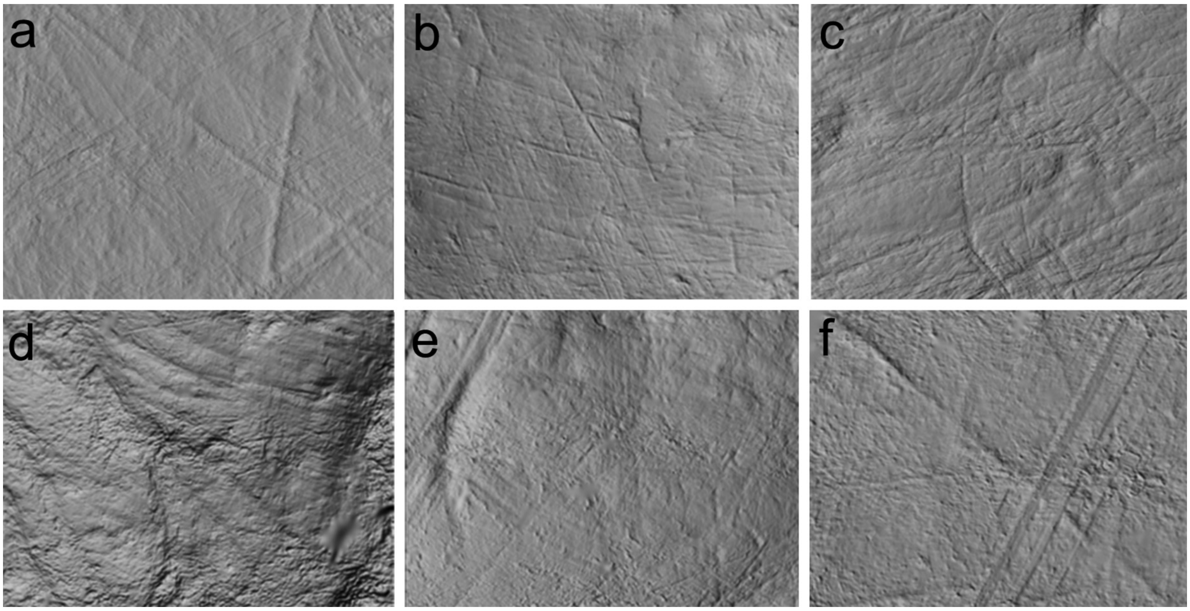

Fig. 1. Two-dimensional photosimulations of occlusal molar texture for (a) Hortus III, (b) Hortus IV, (c) Hortus V, (d) Hortus VI, (e) Hortus VIII and (f) Hortus XI. Note textural similarities between Hortus III and Hortus XI.

Fig. 1. Photosimulations bidimensionnelles de la texture de la surface occlusale de la molaire (a) Hortus III, (b) Hortus IV, (c) Hortus V, (d) Hortus VI, (e) Hortus VIII et (f) Hortus XI. Notons les similarités de texture entre Hortus III et Hortus XI.

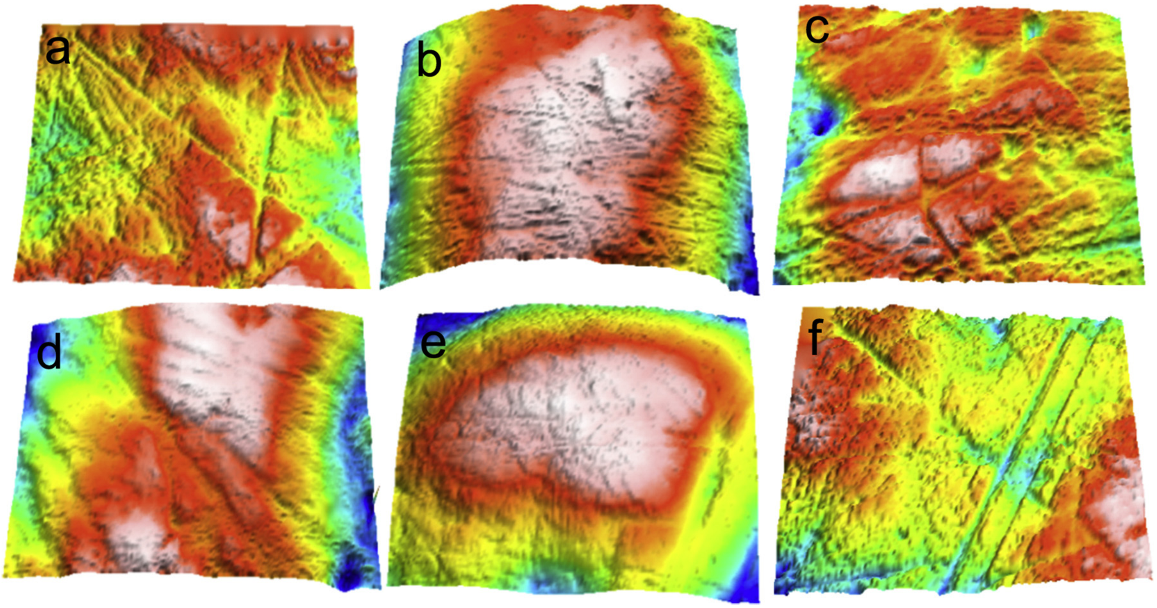

Fig. 2. Three-dimensional enamel surface reconstructions for (a) Hortus III, (b) Hortus IV, (c) Hortus V, (d) Hortus VI, (e) Hortus VIII and (f) Hortus XI. Note textural similarities between Hortus III and Hortus XI.

Fig. 2. Reconstructions tridimensionnelles de la surface de l'émail de (a) Hortus III, (b) Hortus IV, (c) Hortus V, (d) Hortus VI, (e) Hortus VIII et (f) Hortus XI. Notons les similarités de texture entre Hortus III et Hortus XI.

Table 4
Textural variables.
Tableau 4
Variables texturales.

Fossil	Complexity (*Asfc*)	Anisotropy (*epLsar*)	Scale of maximum complexity (*Smc*)	Textural fill volume (*Tfv*)
Hortus III (826)	1.22	0.0009	0.502	26,347.5
Hortus IV (1436)	1.36	0.0051	0.495	48,948.8
Hortus V (693)	1.00	0.0039	0.676	31,866.1
Hortus VI (13)	1.50	0.0041	0.344	42,544.6
Hortus VIII (375)	1.18	0.0047	0.344	53,577.8
Hortus XI (635)	1.54	0.0021	0.496	25,393.64
Kebara 2	0.42	0.0051	3.985	52,425.3
Kůlna 1	1.83	0.0021	1.379	44,919.0
La Quina 5	0.75	0.0024	0.495	40,127.6
Malarnaud	1.01	0.0011	1.114	31,004.4
Montmaurin	1.52	0.0017	0.346	39,483.2
Spy 1	2.22	0.0032	0.690	25,521.0
Tabūn Series III	1.55	0.0018	0.505	13,063.7
Švédův stůl	1.06	0.0022	0.496	30,363.5

convex hull is generated using the outermost values to define a closed set encompassing the smallest possible area demarcated by the entire sample. Two bivariate plots are shown, complexity (*Asfc*) compared to anisotropy (*epLsar*) and scale of maximum complexity (*Smc*) versus textural fill volume (*Tfv*). The Hortus assemblage, grouped with a convex hull, is also compared to a schematic representation of complexity and anisotropy using hunter-gatherers, agriculturalists and pastoralists, including Early Bronze Age England, Late Bronze Age England, Iron Age England, Iron Age Nepal (Mebrak), Bronze and Iron Age Greece, Mongol Xiongnu (Xiongnu Period Mongolia) and Bronze Age/Iron Age Mongolia from Schmidt et al. (2016); Natufian and Neolithic Israel from Chiu et al. (2012); Indiana Middle Woodland, Indiana Middle Woodland East and Indiana Middle to Late Archaic from Frazer (2011); and Kentucky Archaic from Karriger et al. (2016).

3. Results

3.1. Individual variation in dental microwear textures from Hortus cave

Individuals from Hortus fall into two groups for anisotropy (*epLsar*) and textural fill volume (*Tfv*). Those with elevated anisotropy (*epLsar*) include Hortus IV with the highest value, followed by Hortus VIII, Hortus VI and Hortus V (Fig. 3). Those with elevated anisotropy are all near adults or young adults, estimated to be between 17 and 34 years by de Lumley (1973) (Table 2). The second group includes those individuals who are not in the young adult category such as Hortus III aged to 6.5–7.9 years (Ramirez Rozzi, 2005) with the lowest value, and Hortus XI aged to 50+ years (Lumley, 1973) with the second lowest anisotropy value (Fig. 3; Table 4).

These patterns are replicated for textural fill volume (*Tfv*) where young adults Hortus IV, Hortus VI and Hortus VIII are polarized from Hortus III and Hortus XI which exhibit the lowest, nearly identical, values (Table 4; Fig. 4). Hortus V falls between these extremes but is closer to the young/old grouping with relatively low values for textural fill volume (*Tfv*). Young adults Hortus IV and VIII have the highest textural fill volume (*Tfv*) and anisotropy (*epLsar*).

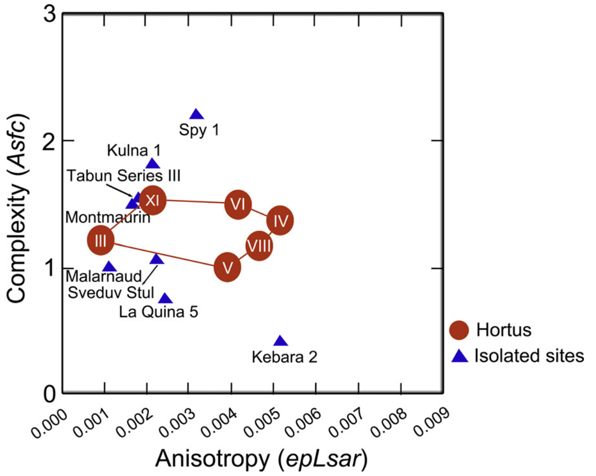

Fig. 3. Bivariate plot of complexity (*Asfc*) versus anisotropy (*epLsar*) for Hortus and Neandertals from isolated sites. A convex hull encompasses 100% of the Hortus sample.

Fig. 3. Graphique bivarié de la complexité (*Asfc*) et de l'anisotropie (*epLsar*) des individus de l'Hortus et de Néandertaliens provenant de différents sites. Une coque convexe englobe 100% de l'échantillon de l'Hortus.

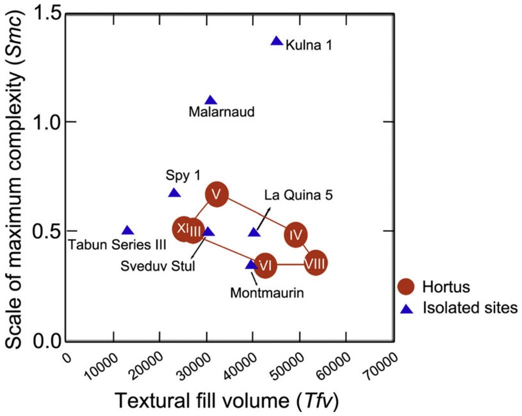

Fig. 4. Bivariate plot of scale of maximum complexity (*Smc*) and textural fill volume (*Tfv*) for Hortus and Neandertals from isolated sites. A convex hull encompasses 100% of the Hortus sample.

Fig. 4. Graphique bivarié de la complexité maximum (*Smc*) et du volume de remplissage textural (*Tfv*) de l'Hortus et de Néandertaliens provenant de différents sites. Une coque convexe englobe 100% de l'échantillon de l'Hortus.

3.2. Comparison of the Hortus assemblage with Neandertals from isolated sites

The Hortus assemblage shows a uniformity of complexity (*Asfc*) and scale of maximum complexity (*Smc*) when compared to isolated Neandertal sites (Figs. 3 and 4). Hortus XI and Hortus VI exhibit elevated complexity (*Asfc*) in the range of Montmaurin and Tabūn Series III, whereas Spy 1 followed by Kůlna 1, are outliers (Fig. 3). In contrast, Hortus V exhibits the lowest complexity (*Asfc*) of the Hortus assemblage which is similar to those of Malarnaud and Svédův stůl, followed by Hortus VIII and Hortus III (Fig. 3). When compared to the isolated sites, Hortus adults exhibit among the highest values for anisotropy (*epLasr*) as well as the lowest, exhibited by Hortus III (Fig. 3). For scale of maximum complexity (*Smc*), the Hortus assemblage contrasts with Kebara 2, which is not shown in Fig. 4 given its extreme value (7.3), followed by Kůlna 1 and Malarnaud (Table 4).

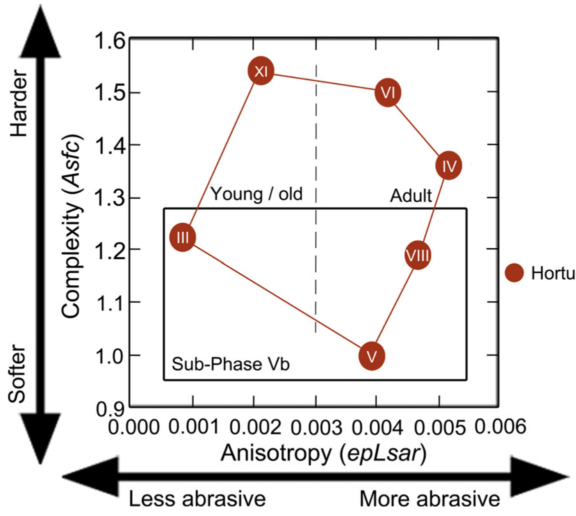

Fig. 5. Bivariate plot of complexity (*Asfc*) versus anisotropy (*epLsar*) for Hortus Neandertals with a convex hull representing 100% of the sample, coupled with a schematic representation (black arrows) of values generated from twelve Holocene societies. Sub-Phase Vb, demarcated by an open rectangle, presented extremes in coldness and aridity and all individuals from this layer of Hortus cave, regardless of life stage, exhibit relatively low complexity (*Asfc*) values.

Fig. 5. Graphique bivarié de la complexité (*Asfc*) et de l'anisotropie (*epLsar*) des Néandertaliens de l'Hortus, avec une coque convexe qui englobe 100% de l'échantillon, couplé à une représentation schématique (flèches noires) des valeurs générées à partir de douze populations de l'Holocène. La sous-phase Vb, délimitée par un rectangle ouvert, présentait des extrêmes de froid et d'aridité et tous les individus de cette couche de la grotte de l'Hortus, quel que soit leur stade de vie, présentent des valeurs de complexité relativement faibles (*Asfc*).

3.3. Comparison of the Hortus assemblage to Holocene humans

All Sub-Phase Vb molars, including Hortus III, Hortus V and Hortus VIII, are characterized by low complexity (*Asfc*) while the others from Hortus cave exhibit higher values (Fig. 5). The lowest complexity (*Asfc*) values for Holocene humans are for pastoralists (Schmidt et al., 2016), followed by Middle/Late Archaic groups from North America as well as Bronze/Iron Age Eurasians (Karriger et al., 2016). Hortus adults largely exceed the published mean anisotropy (*epLsar*) values for agricultural societies, which range from 0.0034 for Neolithic Israel to 0.0041 for Early Bronze Age England, albeit with considerable variability (Karriger et al., 2016). In contrast, the anisotropy (*epLsar*) for Hortus III and Hortus XI resembles those of Holocene hunter-gatherers more than agricultural and pastoral groups (Fig. 5).

4. Discussion

4.1. Comparison of individuals from the sub-phases of Hortus cave

4.1.1. Sub-Phase IVb

Hortus IV from Sub-Phase IVb is from an environment which oscillated between less cold and very cold, and cold-dry conditions as inferred from the dominance of grasses, and the presence of equids. Evidence of sagebrush further indicates a colder habitat than earlier Phase III. However, forests still existed as shown by the presence of voles (Table 1). Correspondingly, a greater degree of plant food consumption compared to later sub-phases is shown in Hortus IV as reflected in elevated complexity (*Asfc*) and textural fill volume (*Tfv*) (Figs. 3–5).

4.1.2. Sub-Phase Va

Sub-Phase Va has been reconstructed as very cold and dry reflected in the dominance of low-lying flowering plants and shrubs, along with thistle and wormwood (Table 1). However, Sub-Phase Va did not experience the extreme cold and aridity characterizing Sub-Phase Vb. Hortus XI from Sub-Phase Va probably had more access to plant foods than available in Sub-Phase Vb given the elevated complexity (*Asfc*) and relatively high value for scale of maximum complexity (*Smc*) (Figs. 3–5). However, Hortus XI exhibits relatively low textual fill volume (*Tfv*). The low anisotropy (*epLsar*) indicates the diet was heterogenous to the extent that the jaw moved in multiple directions. This may indicate a lack of fibrous foods because they tend to require masticatory movements in a common direction.

4.1.3. Sub-Phase Vb

The severe cold and aridity of Sub-Phase Vb (Table 1) correspond to the availability of plant foods, which can exhibit hard and brittle properties, as well as grit which adheres to terrestrial resources. Plant foods would have been fewer given the deteriorating climatic conditions typifying Sub-Phase Vb in which thistle, low-lying flowering plants and sage are the dominant vegetation (Table 1). Consequently, Hortus III, Hortus V and Hortus VIII from Sub-Phase Vb all exhibit low complexity values while Hortus IV and Hortus XI from Sub-Phase IVb and Va, respectively, show much higher textural complexity (Figs. 3 and 5). Complexity (*Asfc*) increases as a function of mastication of plant foods in Holocene humans (Fig. 5) (Schmidt et al., 2016).

4.2. Interpreting dental microwear textures from Hortus cave

It is noteworthy that Hortus III and XI both have the lowest anisotropy (*epLsar*) and textural fill volume (*Tfv*). Only Hortus adults exhibit high values for these two textures. The polarization of the juvenile (Hortus III) and older adult (Hortus XI) compared to young adults suggest that differences in food processing regimes or dietary behavior was based on age. Hortus III is from Sub-Phase Vb and should have been grouped with adults Hortus V and Hortus VIII if only phase explained the results. However, the young adults are grouped regardless of phase, suggesting long-term cultural specializations and/or dietary adaptations. Furthermore, Hortus IV from the earlier relatively warmer and wetter period of Sub-Phase IVb, does not differ substantially in anisotropy (*epLsar*) or textural fill volume (*Tfv*) from other young adults that derive from Sub-Phase Vb, but does differ from older adult Hortus XI from Sub-Phase Va. It might be expected that Hortus IV (Sub-Phase IVb) and Hortus XI (Sub-Phase Va) should be the most similar to one another given their proximity in time (Table 1). However, the opposite is true and these two have disparate textural values, both grouping instead with life stage.

However, these sub-phases are distinct with respect to complexity (*Asfc*). Food hardness was lower in Sub-Phase Vb, a period when extreme cold and aridity prevailed suggesting a greater reliance on softer foods, such as meat (Table 1; Fig. 5). Hortus XI from Sub-Phase Va has the highest degree of complexity of the assemblage and resembles Indiana Middle Woodland societies reconstructed as consuming substantial amounts of nuts and seeds (Frazer, 2011; Karriger et al., 2016).

A principal aim of this study was to examine whether the individuals from Hortus cave cluster together or whether they are dispersed. The dental microwear textures of scale of maximum complexity (*Smc*) do cluster the assemblage from Hortus, whereas complexity, anisotropy and textural fill volume disperse the Hortus assemblage into two relatively distinct groupings. None of the individuals from Hortus are outliers, including Hortus VI, which is unassociated with respect to phase, suggesting that indeed, the assemblage forms a group and where differences are present; they are largely based on age, and to a lesser extent, chronology.

Hortus cave can be reconstructed as exhibiting a Mediterranean climate. The circum-Mediterranean tends to be relatively arid with seasonal rainfall. In many respects, the Hortus assemblage is similar to Kebara 2 and Tabūn Series III indicating an ecogeographic grouping of individuals from the cirum-Mediterranean. Inland climates tended to be colder during MIS 3 and may have relied more heavily on meat (Fiorenza et al., 2011, 2015). Whereas hard food consumption would be expected to increase complexity, lower values would indicate the ingestion of fewer hard foods, such as phytoliths, hard seed shells, marine shells, grit, clay and sand (Calandra et al., 2012; DeSantis et al., 2013; Schmidt et al., 2016). Higher levels of anisotropy (*epLsar*) would indicate a greater reliance on tough foods, such as plant fibers (Karriger et al., 2016). The individuals from Hortus did not have a soft diet with elevated values for textural fill volume (*Tfv*) and, to a lesser degree, complexity (*Asfc*). Like Neandertals from Krapina and Vindija, adults and near adults from Hortus likely processed or consumed tough fibrous foods or fibers (Karriger et al., 2016).

While data on sex is not available for the Hortus sample, differences in non-masticatory anterior dental wear features (Estalrrich and Rosas, 2015) and molar microwear textures (Estalrrich et al., 2017) have been reported among some Neandertals. Extensive non-masticatory wear is well documented in the anterior dentition from Hortus (Estalrrich and Rosas, 2015; Lumley, 1973). At El Sidrón, elevated anisotropy (*epLsar*) among females may correspond to sex-based divisions of non-masticatory or dietary behaviors (Estalrrich et al., 2017) and a similar scenario could explain some of the variation in anisotropy at Hortus.

5. Conclusion

There is evidence that the diet differed between Sub-Phase Vb, which was colder and drier, and the other phases of Hortus cave. Sub-Phase Vb individuals may have had a greater reliance on meat as compared to the diet characterizing Hortus XI, and to a lesser extent, Hortus VI and Hortus IV, all of whom probably included more plant foods. Yet, all the young adults from Hortus appear to have consumed similar kinds of dietary resources or exhibited cultural/preparation regimes in common. Juveniles and older adults may have consumed or processed fewer fibrous and/or tough foods. The dietary repertoire of Hortus was more similar to circum-Mediterranean Neandertals than to continental sites farther north and inland.

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