

**Neandertal Dental Microwear Texture Analysis: A Bioarchaeological
Approach**

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Dr. Christopher W. Schmidt, Advisor

To my parents,

Ann and Thomas Shearon

Who have loved me unconditionally and supported all my academic endeavors

And

To my partner,

Kristen A. Broehl

Who has been an endless source of encouragement, a world-class editor, and my

biggest fan

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1. Introduction

Neandertals are best represented from marine isotope stages (MIS) 6 through 3 (30,000-190,000 BP). During this long period of time, Neandertals successfully occupied areas of western Eurasia and coped with drastic fluctuations in climatic conditions associated with alternating glacial/interglacial cycles of the Middle and Late Pleistocene (van Andel and Tzedakis 1996). Although the fossil and archaeological records indicate that their occupation of Pleistocene western Eurasia may have been discontinuous (Hublin and Roebroeks 2009), significant evidence suggests that Neandertals were environmentally successful. Their remains have been found in several habitats ranging from warm and forested to cold and open. Doubtless, these varying environments would have led to differences and fluctuations in resource availability and would have resulted in highly adaptive Neandertal subsistence patterns. As with geography, temporal changes in diet are key to understanding Neandertal cultural adaptations during the dynamic glacial period in which they flourished. Previous studies of their dental microwear indicate that divergent environments yielded significantly different microwear signatures (El Zaatari et al. 2011). The current study looks for similar evidence of microwear-based dietary differences by focusing on previously unstudied Neandertal remains and taking into account temporal and geographic differences.

Given that previous studies have shown variability in Neandertal diet between ecological regions (e.g., El Zaatari et al. 2011, 2016), this study explores the ways in which microwear disparities manifest themselves with regard to age within a population. Recently, studies using dental microwear texture analysis (DMTA) have effectively detected subtle dietary differences in Middle and Late Pleistocene humans (Estalrich et al. 2017; Remy et al. 2014). Furthermore, comparisons have been made between Neandertals and modern human groups. Archaeological

populations from similar environmental contexts (i.e. the Inuit) mirror those found in some Neandertal groups (Krueger and Ungar 2012). Thus, this project is bioarchaeological; it takes a population-based approach that seeks to determine inter- and intra-population dietary nuances. It also assumes that decisions regarding diet are culturally mitigated and, as such, could vary based on social variables, including demography. In the end, the current study seeks to understand the variability we see in Neandertal dental microwear in relation to where they lived and their biological ages.

1.2 Neandertal diet studies

Attempts to reconstruct Neandertal diet have been carried out using several different techniques, including the analysis of faunal assemblages (Antunes 2000; Aura Tortusa et al. 2002; Barton 2000; Boyle 2000; Conrad and Prindiville 2000; Finlayson et al. 2006; Finlayson et al. 2001; Patou-Mathis 2000); botanical remains (Hardy 2004; Lev et al. 2005; Madella et al. 2002); bone and tooth chemistry (Beauval et al. 2006; Bocherens et al. 1999; Bocherens et al. 2001; Bocherens and Drucker 2003; Bocherens et al. 2005; Bocherens et al. 1991; Fizet et al. 1995; Richards et al. 2000; Richards and Schmitz 2008; Richards et al. 2008; Richards and Trinkaus 2009); SEM-based dental macrowear (Fiorenza 2015; Fiorenza et al. 2011; Fiorenza and Kullmer 2013); dental calculus (Hardy et al. 2012; Henry et al. 2010; Weyrich et al. 2017); and DMTA of incisors (Krueger and Ungar 2012; Krueger et al. Under Review) and molars (El Zaatari et al. 2011; El Zaatari et al. 2016; Estalrich et al. 2017; Perez-Perez et al. 2003).

Zooarchaeological data indicates at least some level of geographic differences associated with Neandertal prey selection. Studies indicate that Neandertals from colder environments in northern and central Europe relied heavily on large-bodied herbivores (Conrad and Prindiville 2000; Patou-Mathis 2000), while those from warmer environments in southern/Mediterranean

Europe increased their reliance on medium-sized herbivores (Aura Tortusa et al. 2002; Boyle 2000). The consumption of small-bodied and marine animals has been found in several Middle Paleolithic sites in Europe's southern/Mediterranean region (Antunes 2000; Barton 2000; Finlayson et al. 2001). These studies may suggest temporal differences in Neandertal diets associated with climatic changes (Conrad and Prindiville 2000; Patou-Mathis 2000). Evidence further indicates plant-food exploitation, based on analyses of floral remains in site sediments (Lev et al. 2005; Madella et al. 2002), tools (Hardy 2004), and dental calculus (Henry et al. 2010).

Stable isotope analyses conducted on 15 Neandertal individuals from different European sites indicate a general conformity in diet (Beauval et al. 2006; Bocherens et al. 1999; Bocherens et al. 2001; Bocherens and Drucker 2003; Bocherens et al. 2005; Bocherens et al. 1991; Fizet et al. 1995; Richards et al. 2000; Richards and Schmitz 2008; Richards et al. 2008; Richards and Trinkaus 2009). All of these individuals' diets consisted almost entirely of meat from large, open-range herbivores, but it should be noted that this statement cannot be applied to all Neandertals because the specimens analyzed came only from northern and central Europe and all date to MIS 3, with one exception (dated to MIS 5) (El Zaatari et al. 2011).

In contrast to the relatively homogenous diet indicated by stable isotope studies, dental macrowear in Neandertals indicates at least some degree of variability. When compared to modern hunter-gatherer populations with known diets, Neandertals show high degrees of dietary variability within Mediterranean evergreen habitats but a more restricted diet in upper latitude steppe/coniferous forest environments, which suggests a high consumption of meat resources (Fiorenza et al. 2011). A later study by Fiorenza (2015) reaffirms the consumption of animal proteins in cold-habitat environments, such as steppe and grasslands, and indicates potential

dietary differences in chronological sequences, where warm periods correspond to higher diversity. Maxillary molar macrowear of the Saccopastore Neandertals also shows some degree of non-normal chewing behavior, suggesting the functional use of the dentition in non-masticatory cultural behaviors (Fiorenza 2015). These wear patterns occur in both Neandertals and early *Homo sapiens* from Near Eastern Middle Paleolithic sites and have been interpreted as using the posterior teeth as tools for tearing, holding, and shaping objects (Fiorenza and Kullmer 2013).

Unlike other lines of evidence whereby diet must be inferred, dental calculus studies provide a uniquely direct insight into Neandertal diet. Calculus collected at Shanidar III (Iraq) and from Spy I and II (Belgium) indicates that Neandertals were exploiting a considerable amount of plant materials including date palms, legumes, and grass seeds, which show damage indicative of cooking (Henry et al. 2010). Results from Spain's El Sidrón site demonstrates the first molecular evidence for inhaling wood-smoke and bitumen and ingesting a wide range of cooked plant materials (Hardy et al. 2012). The El Sidrón case is also particularly significant because it marks the first report of Neandertal use of medicinal plants and supposes advanced knowledge of the surrounding environment and the various plant resources available for exploitation (Hardy et al. 2012). Most recently a study conducted by Weyrich et al. (2017) indicates that the Spy Neandertals were relying on a heavily meat-based diet that included woolly rhinoceros and wild sheep characteristic of the steppe environment they inhabited. In contrast, the El Sidrón Neandertals showed no evidence of meat consumption in their calculus; instead it had dietary components of mushrooms, pine nuts, and moss and reflects forest-based gathering behaviors. This distinction was further reflected in differences in oral bacterial communities between the two groups. The study confirmed the use of medicinal plants by an El Sidrón

Neandertal who suffered from dental abscess and a chronic gastrointestinal pathogen (Weyrich et al. 2017). On the whole, the available calculus data indicate that Neandertals were exploiting meat resources but also had significant plant components in their diet, including those with medicinal properties.

Neandertals are known to have used their anterior teeth in ways that led to extreme wear, creating what is commonly referred to as an “inverse bevel” on their labial surfaces (Ungar et al. 1997). Rounded wear is also common on the anterior teeth, and it has been noted that they are in general more worn than the posterior dentition (Molnar 1972). This phenomenon appears across both time and space in Neandertals, notable examples being Shanidar I (Iraq) and La Ferrassie (France) where crowns have been worn away completely (Heim 1976; Trinkaus 1983).

Neandertal anterior teeth also demonstrate a high frequency of chipping or fracturing (Fox and Frayer 1997). Heavy attrition of the anterior teeth reflects “non-dietary” wear as seen in several different cultures (Molnar 1972). Eskimo cultures are particularly of interest in this regard as they display similarly high rates of wear and chipping, which stem from the use of teeth in cracking and splitting bone, opening mollusk shells, softening animal hides, using the front teeth to clamp one end of an object while it is being worked by the hands at the other end, and using teeth to cut and tear seal meat (Guatelli-Steinberg 2016). Dental microwear texture analysis studies conducted by Kreuger (Under Review) support the conclusion that Neandertals in cold-climate, steppe regions used their anterior dentition in a functional method similar to that of the Eskimo.

Additional indicators of Neandertal dietary variability have been produced through DMTA conducted on buccal tooth surfaces (Perez-Perez et al. 2003). These samples demonstrate high intra-group variability, which correlates with changing paleoenvironmental conditions.

Further studies by El Zaatari et al. (2011), conducted on molar occlusal surfaces, indicate a significant difference between Neandertal groups in wooded areas and those in open-steppe environments, as well as a general increase in consumption of plant materials alongside increases in tree cover. Karriger et al. (2016) reported that DMTA from the Croatian Neandertal groups of Krapina and Vindija was consistent with high-meat foragers, but also indicated that the Krapina Neandertals showed evidence of noteworthy plant consumption in their diet. An intra-group analysis of the El Sidrón Neandertals reveals sex-based differences in microwear; overall their microwear is similar to other Neandertals from wooded habitats and is interpreted as containing a mix of both meat and plant foods (Estalrrich et al. 2017).

Interestingly, Neandertal dietary variations resemble those in humans from more recent archaeological populations. For example, Remy et al. (2014) found sex- and age-based differences in microwear among Roman-era Herculaneum people who were killed simultaneously by a pyroclastic surge from Mt. Vesuvius. Study of this population allowed analysts to see microwear variation within a large, diverse group who died on the same day. Despite the variety of people and huge array of available foods, some patterns emerged between young and old adults as well as males and females. In addition, the children tended to have diets very similar to those of the adults. That contrasts with the Medieval population at Canterbury, where the children tended to have elevated dietary hardness (Mahoney et al. 2016). The important nuances that emerge when looking carefully at intra-site variation in humans show it is prudent to carefully consider intra-site variation seen in Neandertals.

In this study, the Neandertal population of l'Hortus presents a unique instance for a population-based approach. This is particularly encouraging given the previous results from El Sidrón, which found a sex-based difference in microwear texture (Estalrrich et al. 2017).

Although the sample size represented herein is small by bioarchaeological standards, and more typical of paleontological sites, it nonetheless is suitable for detailed intra-site study in order to compare it properly to other sites.

1.3 Microwear texture

Microwear forms on the enamel surface as food and exogenous grit particles impact a tooth primarily during the Power Stroke of the chewing cycle (Ungar 2015). It is important to note that food and grit particles do not have to be harder than enamel in order to create enamel wear (Xia et al. 2015), but they are generally of a hardness at or near it. Recent DMTA studies indicate that meat consumption tends to mitigate microwear formation (El Zaatari 2010). This is not to say that meat creates no microwear features, but fewer of them (Hua et al. 2015). This is supported archaeologically in that populations thought to consume large amounts of meat tend to have low microwear complexities (e.g., Schmidt et al. 2016). Thus, those individuals who consume high quantities of meat are likely to have less overall microwear formation than those who eat less meat and consume foods more likely to form microwear. Dietary reconstructions resulting from DMTA studies are based on surface characteristics including surface complexity, feature orientation, and feature depths that vary depending on the types of foods and the respective quantities of each food being consumed.

1.4 Hypotheses

- 1.) Given previous microwear studies that indicate intra-site dietary nuances (Estalrich et al. 2017), it is hypothesized that DMTA from the site of l'Hortus will show age-based differences in diet.
- 2.) Neandertal DMTA has previously been shown to have an eco-geographic correlation (e.g. El Zaatari et al. 2011). The site of l'Hortus is located in the Mediterranean region of southern

Europe, and it is hypothesized that this group will show continuity with other individuals from this ecological area.

3.) It is hypothesized that the DMTA signature of the Mediterranean ecological region should differ from those found in non-Mediterranean regions (e.g. steppe/tundra and coniferous forests).

4.) It is hypothesized that temporal differences should manifest according to glacial and inter-glacial periods, warmer periods showing continuity with other similarly warm climatic periods.

2. Materials

In total, 17 individuals were included in the current study. I used age determinations from the following sources for each site (de Lumley 1973; Fraipont 1936; Gómez-Olivencia et al. 2009; Howell 1960; Klima 1962; Leroi-Gourhan 1988; Patte 1957; Svoboda 2005; Trinkaus 2016; Twiesselmann 1971). I was only able to assign two age categories: adult and sub-adult.

Temporal designations came from the same sources used for age, and placed each individual into a marine isotope stage (MIS). This means of temporal placement was approximate because absolute dates are not available for each specimen. There are four MIS designations represented by the study group ranging from MIS 6 to MIS 3. Eco-zones data were constructed using deep ice core data provided in Van Andel and Tzedakis (1996). There are two eco-zones designations for this study: the Non-Mediterranean (including both steppe/tundra and coniferous forest environments) and the Mediterranean (which contains brush-like vegetation and some forested areas).

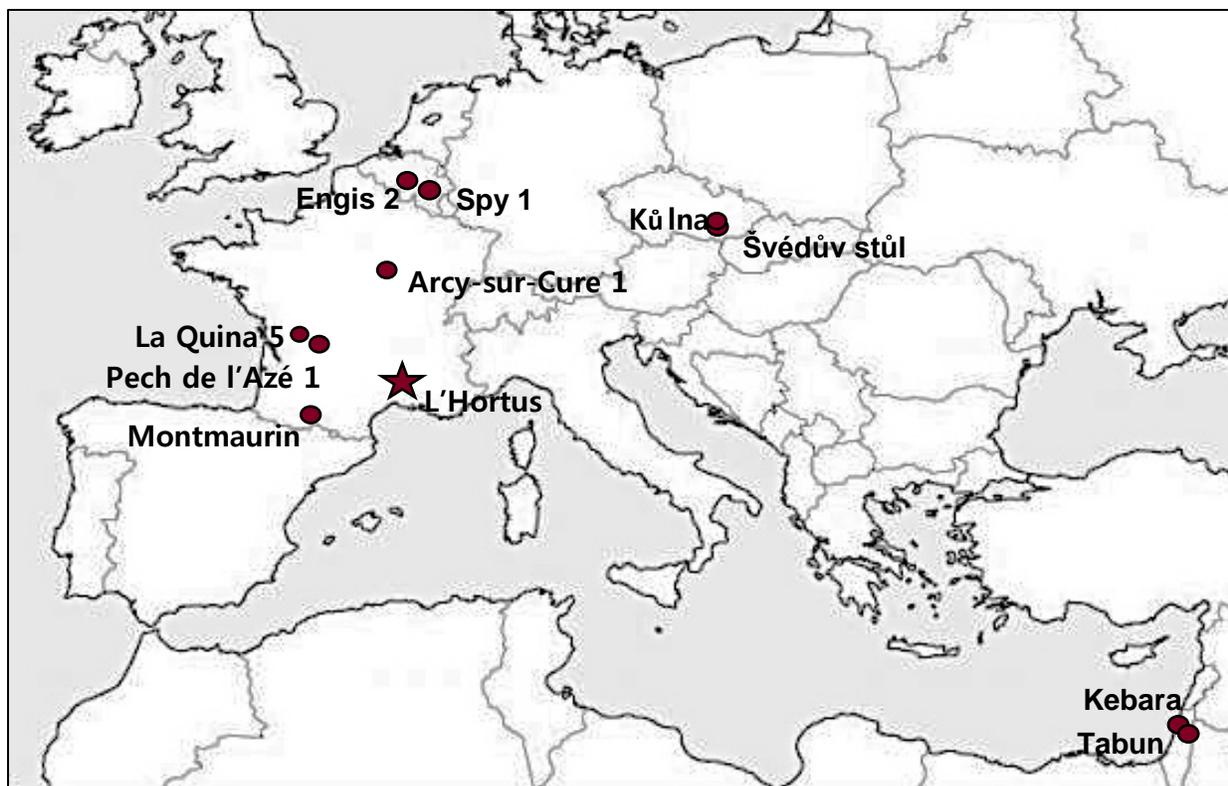


Figure 1: Map depicting the site locations of the specimens included in the study.

2.1 Non-Mediterranean Specimens (n =8)

Arcy-sur-Cure (Grotte du l'Hyène): Arcy-sur-Cure 1 consists of an adult mandible and maxilla. Dates provided by Leroi-Gourhan (1988) based on the presence of gray lemmings (*Lagurus lagurus*) place the specimen within MIS-5b. Similar sedimentary data from the site indicates a cold, open steppe environment (Leroi-Gourhan 1988). This classification is further supported by ice core data from Van Andel and Tzedakis (1996).

Engis: Engis 2 comes from the site of Engis, Belgium, and constitutes the remains of a sub-adult (Fraipont 1936). It is clearly Neandertal, but the MIS it belongs to is unknown.

Kulna: The Kulna I individual consists of four teeth present in a maxilla; its estimated age is 14 years (Svoboda 2005). Since people of this age tend to have an adult diet (and because this

person has no deciduous teeth remaining) for the purposes of this study, this individual is classified as an adult. ESR dating from Kulna Cave dates the remains to $46,000 \pm 6,000$ years old, thus within MIS-3 (Rink et al. 1996).

The faunal assemblage associated with stratum 7a, where the Neandertal remains were found, contains predominantly reindeer, an abundant assemblage of mammoth, and the sporadic occurrence of elk and bovids common of the Wurm (Valoch 1970). Environmental reconstructions from Van Andel and Tzedakis (1996) suggest that the area was largely a steppe environment with interspersed coniferous tree cover (Valoch 1988).

La Quina: The La Quina 5 individual was traditionally assumed to be female, although recent studies suggest that the remains are either male or indeterminate in nature (Trinkaus 2016). Lack of a pelvis makes specific age of this individual difficult to determine, but the remains are definitively adult. Although no absolute dates are available for the layers in which the specimen is contained, relative dating based on absolute dates for higher layers place La Quina 5 in either MIS 3 or 4 (Mercier and Valladas 1998). Reindeer and horse dominate the faunal assemblages, suggesting the prevalence of an open habitat (Henri-Martin 1966). Ice core data provided by Van Andel and Tzedakis (1996) suggest that the area would have been largely tundra/open steppe during this time period.

Montmaurin – La Niche: The Montmaurin mandible is presumably from an adult. The mandible is usually assigned to “Pre-Neandertals” (Howell 1960; Vallois 1955) and has been dated to the end of the Riss Glaciation, approximately 130 kyr BP, placing it within MIS-6 (Grun and Stringer 1991). Pollen analyses from the same stratigraphic layer as the mandible indicate that site vegetation was relatively open-steppe-like but also contained some low

percentage of tree cover dominated by conifers interspersed with deciduous trees (Girard and Renault-Miskovsky 1983; Renault-Miskovsky and Girard 1998).

Pech de l’Azé: The Pech de l’Aze individual is estimated to be 2-3 years of age, hence a sub-adult (Patte 1957); as such, no sex information is available. The remains have been dated to 51,000-41,000 years old and give the specimen temporal designation of MIS-3 (Soressi et al. 2007). Faunal remains from the site indicate that Neandertals there hunted red deer seasonally, which is consistent with a temperate, forested environment (Armand et al. 2001; Rendu 2010). Van Andel and Tzedakis (1996) indicate that this region would have been largely coniferous forest with interspersed deciduous vegetation.

Spy: The Spy 1 individual comes from the site of Spy, Belgium, and is radiocarbon dated to around 36 kyr BP (Finlayson et al. 2006). The individual is believed to be a young adult female (Twisselmann 1971). Horses and reindeer dominate the associated faunal assemblage, indicating open vegetation and cold conditions (Finlayson et al. 2001). These reconstructions are further supported by northern European pollen spectra, which show that an open vegetation (fluctuating between tundra/shrub tundra and steppe-tundra/temperate grassland) prevailed during MIS 3 (Hardy 2010; Lowe and Walker 2014).

Švédův stůl (Ochoz): The Švédův stůl (Ochoz) 1 individual consists of a fragmentary mandible and maxilla of an adult (Klima 1962; Svoboda et al. 1996). The remains and associated assemblages have been dated to MIS-4 (Musil 2003; Svoboda et al. 1996). Faunal remains as well as deep ice core data support the eco-zone designation of coniferous forest (Musil 2003; van Andel and Tzedakis 1996).

2.2 Mediterranean (n=9)

Kebara: The Kebara 2 individual is estimated to be an adult male (Gómez-Olivencia et al. 2009). Thermoluminescence dating places the burial at approximately 60,000 years old (MIS-4) (Valladas et al. 1987). Most common within the faunal assemblage are gazelle (*Gazella gazelle*) and fallow deer (*Dama mesopotamic*), both common within Mediterranean environments, but the site includes other taxa such as horse, red deer, wild boar, and aurochs (Bar-Yosef et al. 1992; Eisenmann 1992; Speth and Tchernov 1998; Speth and Tchernov 2001). Deep ice core data indicate the area would have been typical of a Mediterranean forest/brush environment (van Andel and Tzedakis 1996).

L'Hortus: The site of l'Hortus is represented by six individuals: Hortus III, Hortus IV, Hortus V, Hortus VI, Hortus VIII, and Hortus XI. De Lumley (1973) assigns specific ages for each of the individuals, but, for the purpose of this study and in the interest of accuracy, the designations of sub-adult and adult will be the only categories. Hortus 2 is the only subadult in the assemblage.

The remains of these individuals are dated to an occupation period approximately 60,000-30,000 years ago and are placed in MIS-3 (Lumley et al. 1972). Dating to the Wurmian II period, the site of l'Hortus marks a transition from a cold and wet to a cold and dry climate (Renault-Miskovsky 1972). Pollen studies indicate the area was largely covered by coniferous forests with some evidence of interspersed deciduous trees such as birches and other Mediterranean species (Renault-Miskovsky 1972; Vernet 1973). Faunal remains recovered from the site include those typical of a coniferous forested area, such as ibex and deer, as well as a few more often found in the open steppe, such as woolly rhinoceros and horse (de Lumley 1973).

Tabun: Both Tabun E2 and Tabun Series III are included in the study. The specimens, recovered from stratigraphic layer C, were dated by ESR to between 120 ± 16 kyr and 140 ± 21 kyr BP placing them both within MIS-5 (Grün and Stringer 1991; Mercier and Valladas 2003).

Microfauna from layer C indicates mixed vegetation cover with a dense bush-forest, which was interrupted by grasses and lower vegetation typical of Mediterranean environments (Jelinek et al. 1973). Large mammal assemblages from the site cannot be used in the eco-zone designation because they likely contain a mixture of materials from layers C, D, and B (Jelinek et al. 1973).

Site information coupled with ice core data support the designation of a Mediterranean environment (van Andel and Tzedakis 1996).

Table 1: List of Neandertal specimens sampled in this study. The marine isotope stages (MIS) are inferred from the absolute or relative dates available for each specimen. The eco-zone designation for each specimen represents prevailing conditions during the time of deposition of the Neandertal remains. These classifications are largely derived from Van Andel and Tzedakis (1996), but also draw from sedimentary analyses and floral and/or faunal remains from the same layers/levels as the specimens. Age data for each specimen derives from the primary literature available.

Site	MIS	Individual	Age	Ecozone Designation
Arcy-sur-Cure (Grotte de l'Hyene)	5b	1	Adult	Non-Mediterranean
Engis	---	2	Sub-Adult	Non-Mediterranean
Kulna	3	1	Adult	Non-Mediterranean
La Quina	4	5	Adult	Non-Mediterranean
Montmaurin (La Niche)	6	---	Adult	Non-Mediterranean
Pech de l'Azé	3	1	Sub-Adult	Non-Mediterranean
Spy	3	1	Adult	Non-Mediterranean
Švédův stůl (Ochoz)	4	1	Adult	Non-Mediterranean
L'Hortus	3	III	Sub-Adult	Mediterranean
L'Hortus	3	IV	Adult	Mediterranean
L'Hortus	3	V	Adult	Mediterranean
L'Hortus	3	VI	Adult	Mediterranean
L'Hortus	3	VIII	Adult	Mediterranean
L'Hortus	3	XI	Adult	Mediterranean
Kebara	4	2	Adult	Mediterranean

Tabun	5	E2	Adult	Mediterranean
Tabun	5	Series III	Adult	Mediterranean

3. Methods

In DMTA studies, the focus is placed on second mandibular molar facets because they have been found to be the most useful in distinguishing diet (e.g. (Krueger et al. 2008; Ungar 2011)). The current study included all available molars in order to maximize sample size and is an approach used before in paleontological studies (e.g. Ungar et al. 2012). Therefore, data were collected from maxillary and mandibular first, second, and third molars from the adults as well as from deciduous first and second premolars in the sub-adults. For the molding process, teeth were cleaned using ethyl alcohol (95% ETOH) and a cotton swab to remove any dirt present on the occlusal surface. I molded cleaned teeth with a high-resolution impression material, President's Jet light body, a commonly used polyvinylsiloxane. I then used the molds to create resin casts using Super Hard Epoxy Resin®, an ideal material for creating nearly bubble-free replicas.

1.3 Observing and calculating surface texture

The high-resolution casts were then viewed using a Solarius Sensofar Plμ 2300 (Solarius Development Inc., Sunnyvale, California) white-light confocal profiler (WLCP). I conducted observations within facet 9 on first and second upper and lower molars under a preliminary magnification of 10X. Once an area of interest was located, I collected data at a magnification of 100X (using a 100X-ELWD [extra long working distance lens]) from four contiguous areas covering a total area of 276 x 204 μm. All four areas were then coalesced into a common data cloud through auto-stitching, establishing a total area of 242 x 182 μm. This surface area is slightly smaller than those reported by Ungar and colleagues (e.g., Scott et al. 2012) and is due to

the auto-stitching. This process can reduce study areas up to 10%, but data generated represent the entire area scanned as opposed to collecting data from each quadrant individually.

The data from each specimen were imported into SolarMap® (version 5.1.1), whereby the surfaces were leveled using a least-squares algorithm. Areas on each surface that were deemed unsuitable for study, such as those with adhering particles, were manually removed ('cleaned') using the software. This is an essential part of the process, as the microsurface analysis software is sensitive to surface peaks and valleys. All dirt should be absent from the dataset so that the software does not include it in surface computations. In order to keep surface size for each specimen similar, specimens used in the study had cleaned areas that were less than 10% of their surface area. Any surface deemed to have non-masticatory wear, areas obscured by taphonomy or preservative, or that had more than 10% of the surface removed through cleaning were excluded from analysis.

Data clouds were closely examined as both photosimulations and as 3D representations so as to determine that the surfaces represented true, unobscured microwear features. The 3D representations allowed for observing surface details and aided in determining the validity of certain pits by allowing the analyst to flip the image and study the shape of pits from the underside. Diet-related pits tend to be relatively shallow with a flatter base, while those that are non-diet related (often caused by flaws in casting or molding materials) are extremely deep and terminate in a point (Schmidt et al. 2016). These inspections helped ensure that data clouds were of the highest quality before analysis.

Surface files suitable for analysis were imported into two programs that use scale-sensitive fractal analysis in order to calculate surface characteristics (Scott et al. 2006). The first program was Sfrax®, whereby each file was given a 5% valley suppression, run for textural fill

volume, and saved as an .SDF file. The .SDF files were imported into Toothfrax® software, which calculated the complexity and anisotropy values. Although these procedures are largely identical to those carried out by other DMTA labs, valley suppression is a notable exception. This procedure was undertaken to calibrate the WLCP at the University of Indianapolis with the University of Arkansas profiler and to make sure that cleaned areas were excluded from surface calculations.

3.2. Analysis of texture data

In the present study, the texture variables are area-scale fractal complexity (Asfc), anisotropy (epLsar), and textural fill volume (Tfv). Asfc describes the surface complexity. In this case, more complex surfaces, particularly those dominated by large, deep features, have high Asfc values, while smoother surfaces have lower values. Humans from archaeological contexts tend to have mean population scores between 1.5 and 2 (Schmidt et al. 2016). Low complexity scores are usually below 1, with most groups scoring between 1 and 2 (Chiu et al. 2012; Frazer 2012; Remy et al. 2014; Van Sessen et al. 2013). Exact proportion length-scale anisotropy of relief (epLsar) measures feature orientation; high anisotropy means features are oriented in a common direction. In humans, this value reflects the degree to which the jaw moves in a consistent direction. Diets high in tough, fibrous food and/or homogenous foods (such as domesticates) generate higher anisotropy values, while diets that include harder foods or that are heterogenous generate lower anisotropy values (Chiu et al. 2012; El Zaatari 2010; Frazer 2012). If anisotropy values are contextualized within the available samples from the DENTALWEAR project, high anisotropy values tend to be around .0040, with low anisotropic values being around .0020 (Schmidt et al. 2016). Textural fill volume measures the amount of surface area removed during the creation of

microwear features. Most individuals in the DENTALWEAR project have values that fall between 30,000 and 40,000 (e.g. Chiu et al 2012, Frazer 2012, van Sessen et al 2013, Remy et al 2014).

3.3 Hypothesis Testing

- 1) Age-based DMTA comparisons for l'Hortus are conducted qualitatively due to small sample size.
- 2) Similar qualitative assessments were conducted comparing l'Hortus with the other Neandertals from Mediterranean sites (i.e. Tabun and Kebara).
- 3) ANOVAs were conducted comparing the three DMTA variables (Asfc, epLsar, and Tfv) in Neandertals from the two eco-zone classifications (Non-Mediterranean and Mediterranean).
- 4) An ANOVA was conducted comparing the three DMTA variables (Asfc, epLsar and Tfv) in Neandertals from the four temporal categories (MIS-6, MIS-5, MIS-4, and MIS-3).

4. Results

Table 2: Individual microwear data on the Neandertals analyzed in this study.

Specimen	Tooth	Complexity (A_{sfc})	Anisotropy ($epLsar$)	Textural fill volume (Tfv)
Arcy-sur-Cure 1	LRM1	1.77	0.0008	23829.5
Engis 2	dURM1	1.23	0.0020	60923.0
Kebara 2	LRM2	0.41	0.0051	52425.3
Kulna 1	URM1	1.83	0.0021	44919.0
La Quina 5	LLM1	0.75	0.0024	40127.6
Hortus III	dLRM2	1.22	0.0009	26347.5
Hortus IV	LRM1	1.36	0.0052	48948.8
Hortus V	LLM2	1.00	0.0039	31866.1
Hortus VI	LLM3	1.5	0.0041	42544.6
Hortus VIII	URM1	1.18	0.0047	53577.8
Hortus XI	URM3	1.54	0.0021	25393.6
Montmaurin	LLM1	1.52	0.0017	39483.2
Pech de l'Azé 1	dLRM2	3.73	0.0010	34325.8
Spy 1	LRM2	2.22	0.0032	25521.0
Švédův stůl 1	LLM1	1.06	0.0022	30363.5
Tabun E2	LLM1	1.56	0.0019	13063.7
Tabun Series III	LRM2	0.69	0.0041	29939.6

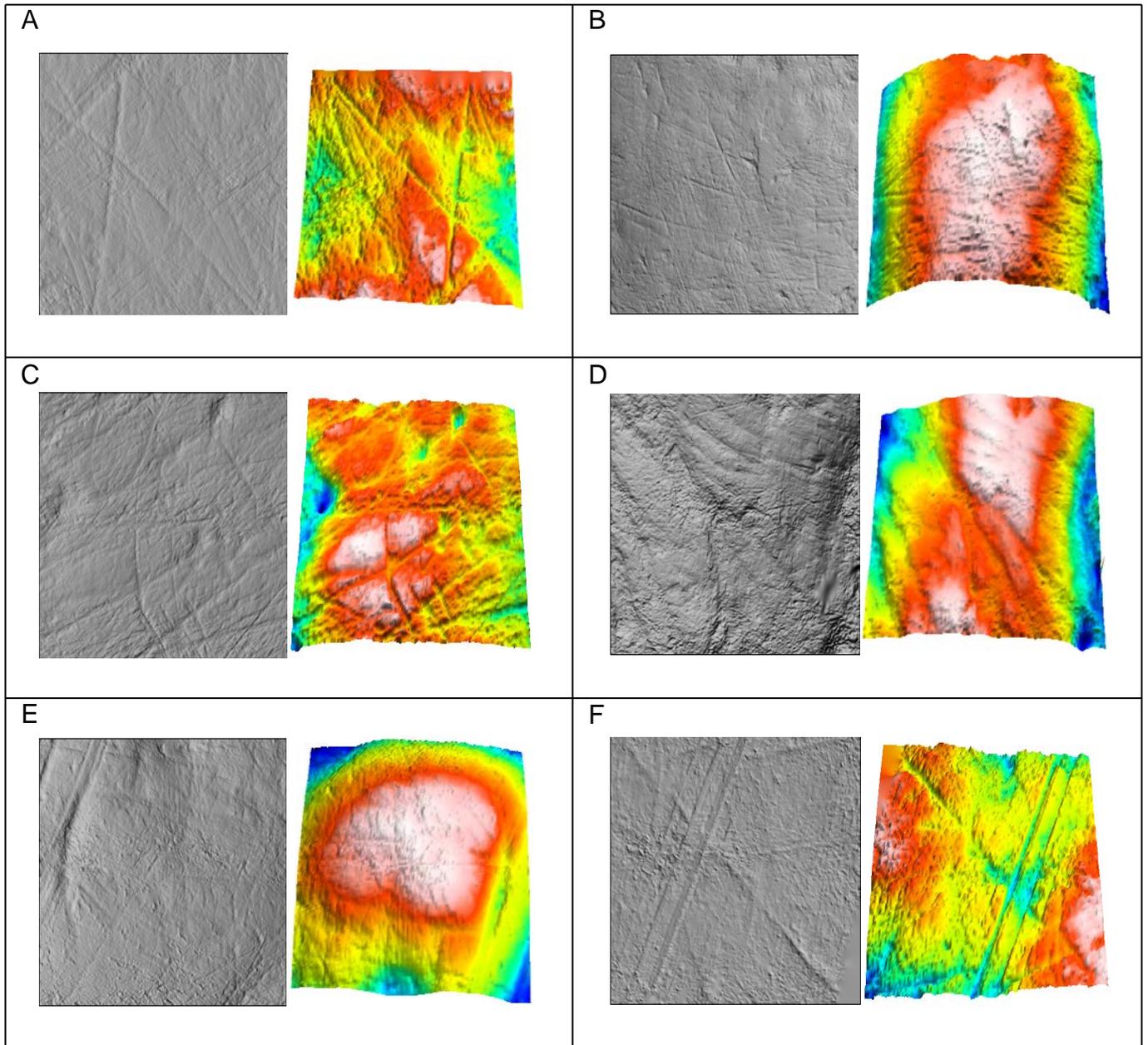


Figure 2: Dental microwear images for the individuals at l'Hortus represented by 2D photo simulations (left) and 3D topographic surfaces (right). (A) Hortus III, (B) Hortus IV, (C) Hortus V, (D) Hortus VI, (E) Hortus VIII, and (F) Hortus XI

Raw data for each of the Neandertal individuals are provided in Table 2. Representative 2D and 3D simulations are provided for each of the l'Hortus individuals in Figure 2.

4.1 Hypothesis 1. DMTA from l'Hortus will show age-based differences in diet.

Within l'Hortus, the adults show much higher anisotropy values ($\bar{x} = 0.0040$) than the sub-adult (Hortus III) (anisotropy = 0.0009) (see Table 2). The sub-adult textural fill volume, of just over 26,000 μm^3 , was within the range for the adults (25,394 - 53,578 μm^3), although toward the low end. Likewise, the sub-adult's complexity was 1.22, which fell within the adult range (1.00 to 1.54). Thus, only the sub-adult anisotropy distinguished it from the adults. The small sample size precludes quantitative analysis, but the difference between the l'Hortus sub-adult and its adult counterparts is notable and on a scale that produces statistically significant differences when encountered in human groups (e.g. Schmidt et al. 2016). Therefore, it is concluded here that an age-based difference is present.

4.2 Hypothesis 2. DMTA from l'Hortus will be similar to other Mediterranean Neandertals.

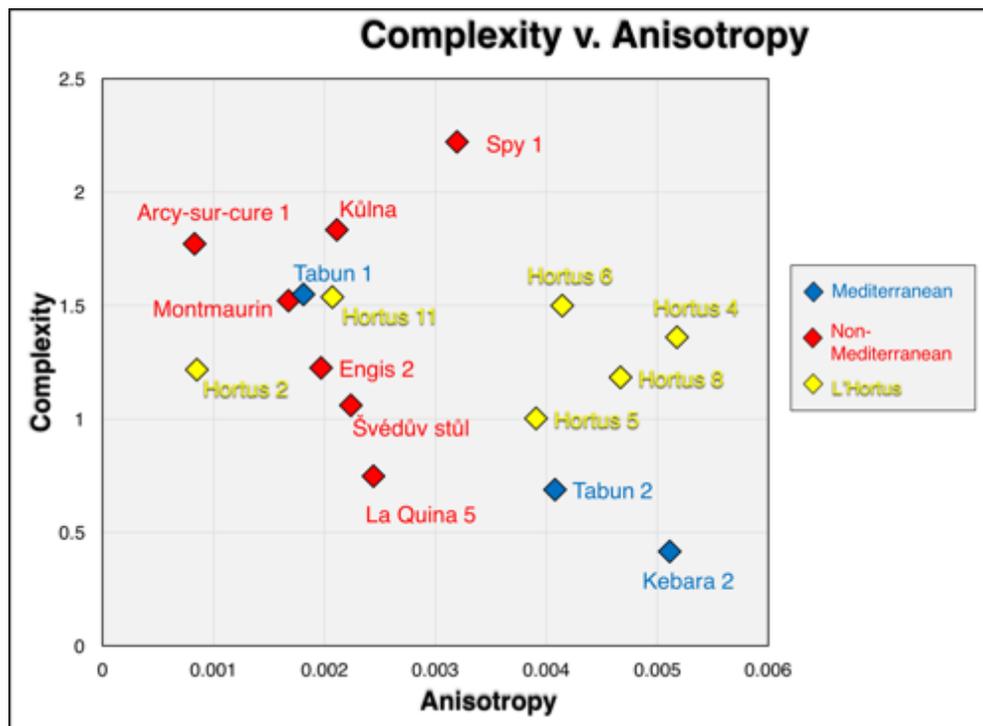


Figure 3: Scatterplot depicting the relative complexity and anisotropy values for the site l'Hortus as well as the comparative Neandertal sample.

The population of l'Hortus (n=6) was then compared to the remaining Mediterranean sample from Kebara and Tabun (n=3). The individuals from l'Hortus show a high anisotropy value ($\bar{x} = 0.0035$) similar to that of Kebara and Tabun ($\bar{x} = 0.0034$). The textural fill volume of the of the l'Hortus population was $38,113 \mu\text{m}^3$ which is similar to the mean for other Mediterranean groups ($\bar{x} = 31,810 \mu\text{m}^3$). Complexity values for l'Hortus ($x = 1.30$) are also slightly higher in value than those for Kebara and Tabun ($x = 0.88$). Therefore, it can be concluded that l'Hortus seems to coincide with other Neandertals from Mediterranean environments particularly in terms of anisotropy (Figure 3).

4.3 Hypothesis 3. DMTA from Mediterranean Neandertals will be different from Non-Mediterranean Groups

Table 3: Mean complexity, anisotropy, and textural fill volume for Mediterranean and Non-Mediterranean Ecozones

	Asfc			epLsar		Tfv	
	N	Mean	SD	Mean	SD	Mean	SD
Mediterranean	9	1.16	0.37	0.0035	0.0015	36012	14030
Non-Mediterranean	8	1.76	0.92	0.0019	0.0008	37437	11987

Table 4: ANOVA output for Mediterranean/Non-Mediterranean Neandertal groups. Significant values ($p < 0.05$) are denoted in bold

		Sum of Squares	df	Mean Square	F	<i>p</i>
Surface Complexity (<i>Asfc</i>)	Between Groups	1.535	1	1.535	3.196	0.094
	Within Groups	7.204	15	0.480		
Anisotropy (<i>epLsar</i>)	Between Groups	0	1	0.000	6.869	0.019
	Within Groups	0	15	0.000		
Textural Fill Volume (<i>Tfv</i>)	Between Groups	8596706.99	1	8596706.99	0.05	0.826
	Within Groups	2580698435	15	172046562.3		

The ANOVA for eco-zone designation showed a significant difference for anisotropy ($p = 0.019$) but not for complexity and textural fill volume (Table 4). Neandertals from Mediterranean areas have, on average significantly higher anisotropy values than those from Non-Mediterranean areas.

4.4 Hypothesis 4. DMTA will differ between temporal categories

Table 5: Mean complexity, anisotropy, and textural fill volume for the temporal designations (MIS-3, MIS-4, MIS-5, MIS-6).

	Asfc			epLsar		Tfv	
	N	Mean	SD	Mean	SD	Mean	SD
MIS-3	9	1.73	0.83	0.0030	0.0016	37,049	10,750
MIS-4	3	0.74	0.32	0.0033	0.0016	40,972	11,055
MIS-5	3	1.34	0.57	0.0022	0.0017	22,278	8,544
MIS-6	1	1.52	---	0.0017	---	39,483	---

Table 6: ANOVA output for temporal designation. No significant values were found.

		Sum of Squares	df	Mean Square	F	<i>p</i>
Surface Complexity (<i>Asfc</i>)	Between Groups	2.266	3	.755	1.412	0.287
	Within Groups	6.422	12	.535		
Anisotropy (<i>epLsar</i>)	Between Groups	0.000	3	0.000	0.425	0.739
	Within Groups	0.000	12	0.000		
Textural Fill Volume (<i>Tfv</i>)	Between Groups	650029381.8	1	216676460.6	1.977	0.171
	Within Groups	1314929967	12	109577497.2		

The ANOVA for temporal designation showed no significant differences in DMTA.

5. Discussion

Table 7: Mean complexity (*Asfc*) and anisotropy for l'Hortus and comparative samples from Holocene *H. sapiens*.

Sample	Subsistence	N	<i>Asfc</i> Mean	SD	<i>epLsar</i> Mean	SD
l'Hortus		6	1.30	0.265	0.0035	0.0017
Natufian, Israel	Prot-Ag	15	1.41	0.645	0.0038	0.0017
Neolithic, Israel	Ag	16	1.34	0.811	0.0034	0.0017
EBA (Early Bronze Age), England	Ag	21	1.34	0.443	0.0041	0.0016
IA (Iron Age), England	Ag	6	1.03	0.342	0.0039	0.0023
Nepal (Mebrak, Sam Dzong)	Ag	10	1.22	0.337	0.0036	0.0013
Greece (Late Bronze/Early Iron Age)	Ag	15	1.14	0.294	0.0036	0.0015
Indiana Archaic (Middle/Late)	Abrasive food H/G	13	1.2	0.306	0.0025	0.0016
Kentucky Archaic (Middle/Late)	Abrasive food H/G	13	1.04	0.158	0.0029	0.0013
Indiana Middle Woodland, East	Hard food H/G	17	1.49	0.535	0.0026	0.0011
Indiana Middle Woodland	Hard food H/G	13	1.52	0.399	0.0021	0.0010
Mongolia, Xiongnu	Past	29	0.92	0.293	0.0035	0.0017
Mongolia, Bronze Age/Iron Age	Past	20	0.93	0.343	0.0033	0.0014
Krapina	Abrasive food H/G	19	1.12	0.580	0.0043	0.0020
Vindija	High meat H/G	4	0.84	0.210	0.0027	0.0031

5.1 Age-based differences in DMTA from l'Hortus

The l'Hortus Neandertal population shows group continuity and forms a relatively cohesive population cluster in terms of DMTA although some nuances, especially with regard to age, are present. *Asfc* shows a moderate value (1.30 on average). That most of the individuals, including the sub-adult, share similar complexity values indicates that diet was consistently modest in hardness. Recall isotope data indicate that Neandertal diets have significant meat components (Bocherens et al. 2001; Bocherens and Drucker 2003; Bocherens et al. 2005). But

the diet is not entirely meat, otherwise the complexity would be much lower; clearly there are enough hard and/or fibrous dietary elements to bring the complexity value to the 1.30 level. Modern *Homo sapiens* who eat high levels of meat and/or dairy products, like Mongolian pastoralists, have complexity values around 1.00 (Schmidt et al. 2016); it is agriculturalists who tend to have complexity values between 1.00 and 1.50 (see Table 7).

The anisotropy values for the l'Hortus Neandertals demonstrate that the l'Hortus adults have elevated anisotropy with an average of 0.0040. This value too is similar to Holocene agriculturalists. But, the l'Hortus sub-adult has an extremely low anisotropy (0.0009), and the oldest individual has an anisotropy of 0.0021 placing it between the sub-adult and younger adults. Therefore, there are some intra-site nuances in diet. Low anisotropy values are associated with a greater variety of foods, such as those exploited by foragers whose jaws move in various directions to accommodate their varied diet (see Table 7). It may be that the sub-adult consumed a soft or heterogeneous diet. For the rest, the similarity between Neandertals and Holocene agriculturalists may suggest that the wild foods Neandertals were eating consisted of USOs, grasses, or sedges that required a consistent jaw movement during consumption. Interestingly, the same high anisotropy is also found at the Neandertal site of Krapina, which is located in a similar Mediterranean environment (Karriger et al. 2016).

In order to address the age-related discrepancy in DMTA at l'Hortus several explanations must be explored including: the implications of differences in enamel thickness which exist between deciduous and adult dentition, potential differences in the biomechanics of adult and sub-adult chew cycles, or the manifestation of biocultural phenomena, such as weaning age dietary transitions or para-masticatory wear.

One potential explanation for the distinct sub-adult microwear values is the differences in enamel thickness which exist between deciduous and adult dentitions. In modern *H. sapiens*, the enamel thickness of deciduous second molars is universally thinner than that which is present on adult first molars (Grine 2005). Even if differences in crown size are considered in the dentition, the trend of thicker enamel in more posterior dentition holds (Mahoney 2013). One hypothesis as to why this trend persists, is that thicker enamel may provide greater resistance to wear (Macho and Spears 1999; Molnar and Gantt 1977; Pampush et al. 2013). This concept appears to correspond with function, where molars, used for grinding, have thicker enamel than incisors, which are used for cutting and shearing (Mahoney 2013). Differences in enamel thickness within a tooth class are explained using the concept of bite force. In this scenario, the jaw acts as a lever during chewing with those teeth which are closer to the fulcrum, in this case the temporomandibular joint, experience more compressive forces as food is processed (Hylander 1975). Interestingly, a study by El Zataari (2010) shows no significant difference in M1 and M2 microwear despite reported differences in enamel thickness, and Perash (2017) found that this trend extends to M3. This suggests that enamel thickness may not contribute meaningfully to differences in DMTA, but further studies examining microwear from individuals with mixed dentitions (containing both deciduous and permanent molars) should be conducted in order to rule out this possibility.

Differences in the mechanics of the chewing cycle between adults and sub-adults below a certain age may also account for the age-based difference seen in l'Hortus. Bite force has been shown to differ significantly between younger and older children as the muscles of mastication gain size and strength with age (Kamegai et al. 2005). A greater bite force would allow for hard particles to be driven more deeply into the enamel as microwear is being formed.

As such, differing bite forces could lead to different signatures in not only between younger and older children but also between children and adults (Kamegai et al. 2005; Mahoney et al. 2016). The way in which the jaw moves during chewing is also worthy of consideration. In children, the reduced size of the mandible will limit the lateral deviation of the jaw. As the mandible increased in size with age, this lateral deviation will increase providing a scenario in which longer scratches might be produced (Mahoney et al. 2016). These long scratches could potentially alter anisotropy values, but this does not necessarily have to be the case.

Hortus III is estimated to be 6-7 years old (Lumley et al. 1972) which coincides with late weaning age in modern *H. sapiens*. Breast-feeding alone will produce no microwear signature, and therefore, it is during weaning period with the introduction of solid foods that microwear will begin to form (Mahoney et al. 2016). The exact time of weaning in Neandertal sub-adults is still uncertain (Humphrey 2010). A look at dental attrition rates indicates that Neandertal sub-adults lag behind Upper Paleolithic anatomically modern humans (UPAMH) up to the age of about 5 years (Skinner 1997). Skinner (1997) suggests that this indicates that dietary supplementation began roughly one year earlier in UPAMH and places the weaning age at approximately 2 years for UPAMH and 3 years for Neandertals. Contradictory results from barium distribution in one sub-adult Neandertal suggest that the weaning process may have begun as early as 7 months with complete cessation at 1.2 years (Austin et al. 2013). Regardless of which estimate is correct, the age of Hortus III indicates that at least some dietary transition is taking place. Mahoney et al. (2016) attributed lower anisotropy values for the ages of 2-4 years in their Medieval sample to the introduction of new items into the diet. Presumably, a more varied diet would result in more varied jaw movements and disorganized chewing. This would lead to the formation of DMTA features in various directions and lower anisotropy values.

Another consideration could be the use of the teeth in non-masticatory activities. The effects of this type of activity on molar occlusal surfaces remain poorly understood (Fiorenza 2015; Fiorenza and Kullmer 2013; Górká et al. 2015), but para-masticatory wear on the posterior dentition (molars and pre-molars) has been documented in several populations ethnographically (Berbesque and Marlowe 2009; Berbesque et al. 2011; Lorkiewicz 2011; Molnar 2008; Molnar 2011; Molnar 1971; Molnar 1972). One way in which para-masticatory wear presents is in the form of grooves on the occlusal surface which are associated with softening and holding fibers in the mouth for the production of baskets and various forms of cordage (Minozzi et al. 2003; Molleson 1994; Schulz 1977; Scott and Jolie 2008), instances of dental chipping and the formation of notches associated with the breaking of hard materials like bone or stone (Scott and Winn 2011), holding objects during the lithic making process (Bonfiglioli 2002), or through contact with wood or bone points used as needles (Bonfiglioli 2002; Bonfiglioli et al. 2004). Estalrich and Rosas (2015) note that Neandertals from El Sidrón, Spy and l'Hortus demonstrate evidence of chipping and labial scratching on the anterior teeth which they attribute to the use of the mouth as a third hand. Although these patterns are demonstrated on the anterior teeth of the l'Hortus adults, the posterior dentition contains none of the macrowear features which indicate para-masticatory processes. Likewise, the use of the dentition in this manner typically leaves distinctive microwear patterns which were not observed in the sample. This makes it unlikely that para-masticatory processes were the cause of the differences in anisotropy between adults and sub-adults at l'Hortus.

5.2 DMTA similarities between l'Hortus and other Mediterranean Neandertals

Within the context of this study, the Mediterranean Neandertals (Kebara, Tabun, l'Hortus) showed moderate complexity values and high anisotropy indicating that this group

consumed tough or homogenous plant foods and relatively few hard foods. As previously mentioned, this trend also extends to the Krapina Neandertals who inhabited a similar Mediterranean environment (Karriger et al. 2016) (See Figure 4 below). Higher anisotropy values are typically indicative of increased plant consumption and appear to be a signature of this environment. This is perhaps not surprising given that the Mediterranean during this time period was conducive to not only increased presence of plant resource but also greater varieties (Tzedakis and Bennett 1995). It follows that, given the relative stability of this environment across time and space, dietary strategies would have developed in a way which encouraged the exploitation of a wide range of the available plant resources.

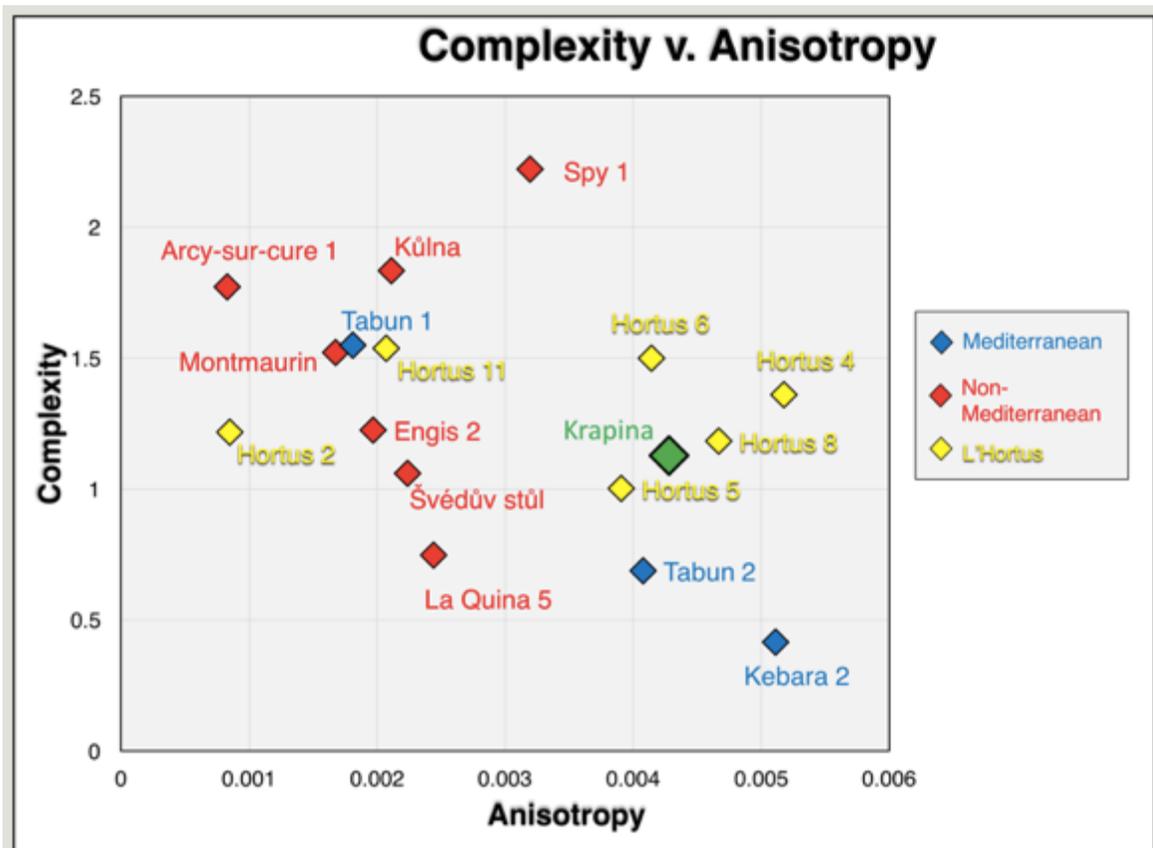


Figure 4: Scatterplot depicting the mean DMTA values of the Krapina Neandertals with the Neandertals for this study.

5.3 The Mediterranean as a distinct ecological zone

The late Middle and early Late Pleistocene in western Eurasia were marked by dramatic climate fluctuations. This in turn forced the Neandertals who inhabited these areas to adapt their dietary strategies in order to survive. Studies of floral and faunal remains from this period indicate that the distributions of both plants and animals were greatly affected by changing environmental conditions. In general, during times of glacial stadial, cold-adapted plant and animal species dominated over warm-adapted ones, while the opposite was true during interglacial and interstadial times (van Andel and Tzedakis 1996). Reconstructions of climate over time indicate that, in any given MIS, Western Europe and the Mediterranean could be divided into several ecological areas. In this study, areas which include southern Europe and the Levant, designated as Mediterranean, were shown to be a distinct environment. Northern areas witnessed local extinctions of plant and animal species, their retreat to more favorable environments during cold periods and re-colonization during warm periods. Mediterranean Europe, on the other hand, is characterized by more ecological continuity over time since glacial advance never affected this region.

Although this study indicates that ecological differences correspond with a more fibrous diet in Mediterranean Neandertals, a holistic view of diet incorporating microwear, dental calculus, microwear and stable isotopes must be implemented to assess its credibility. Dental microwear shows similar differences in wear with regard to region, with Neandertals from Mediterranean environments indicating a high degree of dietary variability in relation to other Neandertals from cold habitats (Fiorenza 2015; Fiorenza et al. 2011). Dental calculus also indicates that Neandertals from areas with more tree cover will exploit more plant materials than those from steppe/tundra habitats (Hardy et al. 2012; Henry et al. 2010; Weyrich et al. 2017). El

Zaatari (2011; 2016) also indicates an increased consumption of plants in more wooded environments, but it should be noted here that the elevated anisotropy values of l'Hortus, Kebara and Tabun are unique to this study and the data presented for the Krapina Neandertals (Karriger et al. 2016). Stable isotopes constitute the only area which appears to contradict the data provided here that suggests increased plant consumption (Bocherens et al. 1999; Bocherens et al. 2001; Bocherens and Drucker 2003; Bocherens et al. 2005; Bocherens et al. 1991; Fizet et al. 1995; Richards et al. 2000; Richards and Schmitz 2008; Richards and Trinkaus 2009). This is likely a result of the ecological context of the Neandertals included in these studies, which were mostly from Non-Mediterranean individuals and would have been more meat-dependent than their Mediterranean counterparts. Further isotopes studies which focus on Mediterranean samples should be conducted in order to confirm this hypothesis, but the DMTA data presented in this study largely corroborate previous studies which indicate dietary nuances between ecological regions and increased plant consumption in areas which contain more tree cover.

5.4 Differences in DMTA are not due to temporal differences

This study failed to detect any significant difference between later and earlier Neandertals. This finding is not unexpected because there is (1) a known association between climatic change, environment, and availability and variety of food resources present and (2) paleoclimate data which suggest that climate change in Eurasia during the time period from MIS-6 to MIS-3 was not a consistent change towards either warm or cold conditions but alternated between warm and cold phases (van Andel and Tzedakis 1996). The representative sample for each temporal category included individuals from a variety of ecological regions. Since dietary differences between ecological regions have already been detected, it follows that a comparison

of means which does not discriminate based on environment would merely compare average DMTA values across regions yielding a relatively homogenous group with regard to time.

6. Conclusions

In conclusion, a qualitative analysis of the l'Hortus Neandertals yielded age-based differences in diet between the Hortus 2 and the adult Neandertals from the site. While complexity values are cohesive for the group and indicate a diet of modest hardness, anisotropy values demonstrate that the l'Hortus adults are consuming a considerable amount of fibrous foods (i.e. tubers, grasses, and other botanicals) but the sub-adult is not. The trend of elevated anisotropy holds for the other Mediterranean Neandertals present in the study (Kebara, Tabun Series III, Tabun E2) as well as the Krapina Neandertals and suggests regional continuity in diet among these groups. Furthermore, Mediterranean Neandertals show dental microwear textures that indicate significantly more plant consumption than Neandertals from northern Europe. No temporal differences were found within the sample.

The study provides additional information to the growing body of data indicating that Neandertals had complex diets. Furthermore, the study provides support for the effectiveness of bioarchaeological models in detecting differences within and between Neandertal populations. Although the much remains to be explained in regard to Neandertal behavior, subsistence strategies and regionalisms, evidence suggests that Neandertals exploited a broad range of available resources within their environments and that these trends extend across time and space.

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