Dental Microwear Texture Analysis of Croatian Neandertal Molars

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ABSTRACT

The present study employs dental microwear texture analysis (DMTA) on molar occlusal surfaces from the Croatian Neandertal sites of Krapina and Vindija to gain greater insight into their diets. Dental microwear texture analysis (DMTA) data were gathered from 19 molars from Krapina and 4 molars from Vindija using white-light confocal microscopy. The scale-sensitive software packages Toothfrax and Sfrax were used to characterize the texture data. The variables used included complexity (Asfc), anisotropy (epLsar), and textural fill volume (Tfv). Based on previous DMTA studies as well as data from analyses of Neandertal calculus, we hypothesized that Vindija and Krapina would have texture values consistent with high meat eaters. Our results indicate that, when compared to Holocene human DMTA data, Vindija and Krapina had relatively low Asfc values (0.84 and 1.12, respectively), which indicates a low surface relief that is consistent with other high meat eaters. While Vindija also had relatively low epLsar (0.0027), Krapina had unusually high epLsar (0.0043) indicating their diet was particularly tough or fibrous. Finally, Vindija had higher Tfv (46,367) than Krapina (35,518), indicating that the Vindija wear features were larger than those of Krapina. We conclude that the diet of the Vindija Neandertals likely contained few hard, brittle foods such as nuts or seeds. The diet of the Krapina Neandertals was more fibrous than that of the Vindija Neandertals, possibly indicating consumption of grasses, tubers, or other unprocessed plants. The results of this study indicate that Krapina and Vindija microwear textures are consistent with high meat consumption, but also indicate that fibrous resources played an important role in their diet.

INTRODUCTION

Neandertal diet has long been a topic of investigation among paleoanthropologists. One reason for this is that dietary differences between Neandertals and modern humans have been invoked to explain the Neandertal disappearance following the arrival of modern humans in Europe. Neandertals long have been considered skilled hunters of Pleistocene animals, based primarily on the copious numbers of Pleistocene faunal remains found in their sites (e.g., Boule 1921; Obermaier 1912; Osborn 1915; Sollas 1911); but in the 1980s, Binford (1985, 1989) argued that, despite this association, Neandertals were likely primarily scavengers rather than effective, organized hunters. Although it is difficult to draw a sharp boundary between scavenging and hunting, recent assessments of faunal samples associated with Neandertals have effectively challenged Binford's claims and reaffirmed the hunting acumen of Neandertals (e.g., Bocherens 2011; Conard and Prindiville 2000; Gaudzinski-Windheuser and Kindler 2012; Gaudzinski-Windheuser and Roebroeks 2011; Germonpré et al. 2014; Miracle 2007; Münzel and Conard 2004; Niven et al. 2012; Stiner 1994). Additionally, Richards and colleagues (2000) demonstrated that a primary scavenging adaptation was not an option for Neandertals based on energetic grounds, while Wißing and colleagues (2015) reach the same conclusion based on the unique aspects of Neandertals' stable isotope signature in northwestern Europe.

The current abundance of evidence for meat consumption has led some paleoanthropologists to suggest that Neandertals relied very little, if at all, on plant or marine resources as dietary components. Instead, Neandertals have been portrayed as top-level carnivores. Early modern humans moving into Eurasia, though, were thought to have made use of a much wider variety of resources (Kuhn and Stiner 2006; O'Connell 2006). It has been hypothesized that this difference in resource utilization contributed to Nean-

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dertal extinction at the hands of contemporary anatomically modern populations (e.g., O'Connell 2006). This may seem like a sufficient explanation, but it is becoming clearer that this simple dichotomy of Neandertals being top-level carnivores and anatomically modern humans being more omnivorous and more adaptable to a wide range of environments oversimplifies dietary and adaptive differences between these two groups (Bocherens 2011; Wißing et al. 2015).

PREVIOUS DIETARY ANALYSES

Analyses of stone tool microwear and residues, faunal materials, and C and N stable isotopes over the past two decades indicate that Neandertals did consume significant amounts of meat. It is particularly the stable isotope analyses that fail to identify plant resources in Neandertal diet. Stable isotopes from fossil hominins indicate the source of dietary protein including terrestrial and marine animals, plants, or some combination of those sources, if comparative faunal samples are available for calibration (Beauval et al. 2006; Bocherens 2011; Bocherens et al. 1991, 2001, 2005; Fizet et al. 1995; Richards et al. 2000, 2008; Richards and Schmitz 2008; Schmitz et al. 2002). Many researchers concluded in the past that Neandertals were top-level carnivores whose dietary protein was derived almost exclusively from meat (Bocherens 2011; Richards et al. 2000; Richards and Trinkaus 2009) with some variation in preferred herbivorous prey by region (Bocherens 2011; Patou-Mathis 2000; Valensi and Psathi 2004; Wißing et al. 2015). Stable isotope ratios indicate that marine and plant resources were not consumed in significant amounts (Bocherens 2011; Richards et al. 2000; Richards and Trinkaus 2009), although archaeological data indicates that marine resources were utilized by Neandertals in some cases (Cortés-Sánchez et al. 2011).

Stable isotope analyses are extremely useful for determining the major source(s) of protein in Neandertal diet, but they are limited in that they may miss other significant sources of nutrition that contain little to no protein (Richards and Trinkaus 2009). As is noted by Wißing and colleagues (2015), isotopic variation between the end points of a dietary line from total herbivory to total carnivory is not linear: inclusion of even a small amount of meat will markedly increase $\delta\,^{15}$N values in a taxon. Bocherens (2009) has shown that inclusion of as much as 50% of plant protein in an omnivore diet results in $\delta\,^{15}$N values that are only around one standard deviation lower than the collagen of a pure carnivore. Thus, even though the signature of Neandertals is consistently high $\delta\,^{15}$N values, this could mask significant amounts of plant nutrients in the diet. Additionally, given that Neandertals were spread across a wide geographical area, they likely lived in a variety of environments. It is not unreasonable to expect that Neandertal diets were dependent upon the environment in which they lived and therefore were not homogenous through time and space. In fact, recent research is indicating that Neandertals diets reflected the environments in which they lived and, at times, included both plant and marine resources. For example, in an examination of residues on stone tools from the site of Payre in France, Hardy and Moncel (2011) found evidence for the processing of terrestrial herbivore meat, wood, fish, birds, starchy plants, bone, and hides. Additionally, marine resources such as limpets, bivalves, sea urchins, fish, monk seals, and dolphins, as well as small game, birds, and rabbits, appear to have been exploited at Gorham's and Vanguard Caves in Gibraltar (Brown et al. 2011). Based on this evidence, Brown and colleagues (2011) concluded that like anatomically modern humans in later occupations of the site, Neandertals took advantage of a range of resources available in the diverse habitats in the area.

Comparative dental microwear analyses of Neandertal samples provide additional support for the hypothesis that their diet was not homogenous across time and space (El Zaatari 2007; El Zaatari et al. 2011). Aspects of Neandertal dental microwear values varied by ecogeographic region, with Neandertals from wooded environments exhibiting higher surface complexity (the change in surface roughness at different scales), and higher heterogeneity (the constancy of surface relief) than Neandertals from open environments. Neandertals from mixed environments more closely matched those from open environments in surface complexity, but in heterogeneity, they more closely matched Neandertals from wooded environments. These results indicate that plants formed a more important part of Neandertal diet in mixed and wooded habitats than in open habitats (El Zaatari 2007; El Zaatari et al. 2011). The present study adds to the available microwear texture data by providing texture values for the Neandertals from Krapina and Vindija in Croatia. Texture values from Vindija were previously investigated (El Zaatari 2007; El Zaatari et al. 2011), but these analyses utilized different equipment. As discussed below, currently it is important to compare results done only on the same equipment.

Dental microwear and stone tool residues are not the only evidence for plant utilization in Neandertals. Preserved phytoliths provide evidence for the utilization of plants, possibly as dietary resources, and have been investigated at Kebara Cave where Lev and colleagues (2005) suggested charred plant remains may have been cooked for food. Additionally, Henry and colleagues (2011) found preserved plant microfossils in Neandertal dental calculus at Shanidar Cave, Iraq, and Spy Cave, Belgium. Just as at Kebara Cave, Henry and colleagues (2011) found evidence that some plants may have been cooked. Hardy and colleagues (2012) undertook both morphological and chemical analyses on dental calculus from Neandertals at El Sidrón and also found evidence for consumption of cooked plant material. In another study, Henry and colleagues (2014) examined both Neandertal and early modern human dental calculus and residues from associated stone tools and found that both populations utilized plant resources. Analyses of fecal matter from El Salt in Spain have also indicated that although Neandertals consumed large amounts of meat, they consumed significant plant material as well (Sistiaga et al. 2014). These studies support the conclusion that even though there may have been dietary differences between Neandertal and modern human populations, the differences were more complex than a simple meat-eating Neandertal, more omnivorous modern human dichotomy (Henry et al. 2014).

Lastly, it may be useful to consider whether Neandertals could have obtained all necessary nutrients by consuming meat alone to the exclusion of plants and/or marine resources. The robust characteristics of Neandertal post-cranial skeletons are suggestive of high levels of physical activity that would have required high levels of energy, which may have been obtained through efficient foraging (Sorensen and Leonard 2001; Smith 2015). Neandertals would have had to, at least at times, endure harsh environments. They may have adapted to these environments through elevated metabolic heat production (Churchill 2006, 2014; Froehle et al. 2013), or through genetic adaptations and increased amounts of brown adipose tissue (Steegman et al. 2002). These factors could have affected Neandertal life history (Snodgrass and Leonard 2009), and dietary requirements (Smith 2013). Froehle and colleagues (2013) show that, based on their body form and adaptations to cold and high levels of energy expenditure, Neandertals would have required a substantially higher basal metabolic rate than modern humans. This would have required a significantly higher caloric intake to support. While meat would have certainly played an important role in meeting this need, it is likely that Neandertals would have made use of any calorie-providing resource available to them, including available plant remains.

DENTAL MICROWEAR TEXTURE ANALYSIS

Dental microwear texture analysis (DMTA) using white-light confocal microscopy has been conducted on a variety of modern human archaeological samples (Beach and Schmidt 2013; Chiu et al. 2012; El Zaatari 2007; El Zaatari et al. 2011; Krueger and Ungar 2010; Mahoney et al. 2016; Schmidt et al. 2011; Schmidt et al. 2016; Van Sessen et al. 2013), fossil hominins (El Zaatari 2007; El Zaatari et al. 2011; Krueger 2011; Krueger and Ungar 2012; Scott et al. 2005; Ungar et al. 2006, 2010, 2011), and non-human primates (e.g., Scott et al. 2009, 2012). For example, in an analysis of anterior tooth wear in Neandertals, Krueger (2011) found that extreme attrition observed in Neandertal anterior teeth varied with climate, location, and oxygen isotope stage. In some cases, the wear was a result of extramasticatory use of teeth as tools to aid in activities such as clamping or grasping, while in other cases, the abrasive load of the diet contributed more to anterior tooth wear (Krueger 2011). A subsequent study (Kruger and Ungar 2012), found that the Krapina anterior teeth exhibited more wear from the abrasive load of their diet than from non-masticatory use. Similarly, El Zaatari (2007) and El Zaatari and colleagues (2011) found that DMTA results varied by ecogeographic region, something also reported by Fiorenza and colleagues (2011).

Criticisms of DMTA's efficacy suggest that it reflects, at best, ambiguous representations of diet that formed days or weeks before death (e.g., Strait et al. 2013). Additionally, some believe that microwear features only form when enamel is impacted by materials harder than it is (e.g., Lucas et al. 2013). Recent experimental work, however, demonstrates DMTA's ability to reflect what is eaten based upon the jaw movement required to masticate it. Hua and colleagues (2015) used a mastication simulator to conduct controlled experiments of tooth wear. They determined that jaw movement perpendicular to the occlusal plane generated more pits, while oblique jaw movements generated more scratches. This is consistent with jaw movements necessary for masticating hard foods and fibrous foods, respectively. They also found that meat created almost no wear and that grit particles of various sizes readily generated wear features. A separate study by Xia and colleagues (2015) determined that foods need not be as hard as enamel to create microfeatures. The hydroxyapatite crystallites comprising enamel are held together by proteins; breaking the protein bonds, rather than damaging the crystallites themselves is all that is required to generate microwear. Finally, while it is true that microwear reflects the diet a few days or weeks before death, this is not always a liability. In fact, the amount of time reflected in microwear differs based upon the diet's hardness and/or abrasiveness—harder diets and those that are very abrasive will have more microwear turnover than softer and/or less abrasive ones (e.g., Grine 1986; Schmidt 2010).

Non-dietary (e.g., extramasticatory) tooth use also creates microwear (Krueger 2011), which can obscure that formed by mastication. However, extramasticatory wear tends to focus on anterior teeth, which are commonly used as tools—a condition particularly well known among Neandertals (e.g., Krueger 2011). Neandertal incisors commonly have an inverse bevel where their labial aspects have wear exceeding that of their lingual aspects. This condition has been attributed to their being used as tools (e.g., Cartmill and Smith 2009; Krueger 2011). Nonetheless, Neandertal molars are generally regarded as bearing suitable masticatory wear and have been studied previously for their macrowear and microwear (e.g., El Zaatari et al. 2011; Fiorenza et al. 2011).

MATERIALS AND METHODS

The current study uses a white-light confocal profiler (WLCP), which has low operating costs and improved inter-observer repeatability compared to scanning electron microscopy and optical light microscopy (Scott et al. 2005, 2006; Ungar et al. 2008). Additionally, one can calculate feature volume using DMTA, something that has not been possible with traditional SEM-based microwear approaches or optical light microscopy (Scott et al. 2006; Ungar et al. 2003, 2008).

Molars from two Neandertal sites, Vindija and Krapina, were used in this analysis. Both sites are located in the Zagorje region (Hrvatsko Zagorje) of northern Croatia. Based on faunal analyses and given their proximity to one another, both sites were likely surrounded by a variety of environments, e.g., open forest/parkland, wetland, rocky, and running water (Miracle 2007; Miracle et al. 2010). The first site, Vindija, has been investigated by other researchers using this technique (El Zaatari 2007; El Zaatari et al. 2011). However, it is important for the current study to collect Vindija data using the same WLCP that was used for Krapina. This WLCP is nicknamed "Indie" and housed at the University of Indianapolis. A recent study by Arman et al. (2016) found that WLCP data can vary somewhat because of nuances in data collection employed by each machine. Arman et al. (2016) propose a data filter that ultimately will standardize data and improve inter-machine comparability, but for the current study it was necessary to independently collect Vindija data. It is important to include Vindija in the current study because it allows for comparisons with the Krapina data collected by "Indie."

Vindija is an important site as it contains the latest evidence for Neandertal fossil remains in Europe (Ahern et al. 2013; Janković et al. 2011) and is one of the sites from which Neandertal ancient DNA has been extracted for analysis and genome sequencing (Green et al. 2010). A series of excavations at the site yielded fossil hominins, faunal remains, and Mousterian, Aurignacian, and Gravettian stone tools (Karavanić 1995; Karavanić and Smith 1998). All of the molars from Vindija are from Level G3, which yielded an AMS radiocarbon date of >42,000 years and a U/Th date from cave bear bones of 41,000+1,000/-900 years (Ahern et al. 2004; Krings et al. 2000; Wild et al. 2001). All other dates from complex G are from other layers within that complex, but these other dates are not relevant for the specimens used in this study. Although more than five molars are present in the collection, some belong to the same individual. Collecting data from more than one tooth from a single individual would bias the results. Thus only five molars were available for data collection and analysis at Vindija.

The second site, Krapina, is a sandstone rockshelter (Karavanić 2004; Smith 1976) that was excavated by Dragutin Gorjanović-Kramberger from 1899 through 1905 (Gorjanović-Kramberger 1906). These excavations yielded over 1,200 Neandertal skeletal elements in addition to a large collection of stone tools and faunal remains (Gorjanović-Kramberger 1906; Miracle, 2007; Smith 1976). Electron spin resonance dates on fossil Merck's rhinoceros (*Stephanorhinus kirchbergensis)* teeth place the site at 130,000±10,000 years (Rink et al. 1995), and it has been suggested that the site was used as a shelter by Neandertals over a period of approximately 20,000 years (Miracle 2007).

The large collection of teeth from Krapina makes it ideal for microwear analysis. There are 199 isolated teeth in the collection, along with numerous others still associated with mandibles and maxillae (Gorjanović-Kramberger 1906; Radovčić et al. 1988; Smith 1976; Wolpoff 1979). Only the unassociated molars were available for this analysis. After excluding all damaged or incompletely formed molars from the collection, 40 isolated permanent molars were molded and examined for dental microwear. Since none of the molars examined in this study were associated with a mandible or maxilla, there is some possibility that some of the teeth studied came from the same individual. Without a way to definitively assess whether any individuals were repeated in this sample, we included all available molars to maximize sample size.

Traditionally, second mandibular molar Phase II facets are examined because they are most useful in distinguishing samples with different diets (e.g., Krueger et al. 2008). Since all available, well-preserved molars were examined in this study to maximize sample size, data came from maxillary and mandibular first, second, and third molars. Teeth were cleaned using ethyl alcohol (95% ETOH) and a soft-bristled toothbrush to remove any dirt that was present on the occlusal surface. Prior to analysis, surfaces were examined microscopically for brush marks. None were found. Next, high-resolution impressions of the occlusal surfaces were made using President's Jet polyvinylsiloxane dental molding material. Once hardened, the impressions were removed and used to create high-resolution epoxy resin casts (Super Hard Epoxy Resin®).

The current study employed a Sensofar Plμ 2300 (Solarius Development Inc., Sunnyvale, California) white-light confocal profiler (WLCP) to generate surface representations from the casts (Scott et al. 2005, 2006; Ungar et al. 2008). This device is designed to conduct superior metrology of surfaces with relief comparable to that found on teeth. It is employed here as a non-contact profilometer that collects data in a series of vertical planes. Target areas were located using a 10x objective lens. Data collection used a Nikon 100x extra-long working distance lens. At this magnification, the vertical (Z) spacing was 0.20μm and the horizontal spacing (X and Y) was 0.16μm. Analysts collected data from four contiguous areas that were automatically stitched together for a total study area approximating 242.03μm X 181.60μm for each tooth. This dimension is somewhat smaller than the study areas described by Ungar and colleagues (e.g., Scott et al. 2012). The difference is due to the autostitching, which reduces study areas up to 10%. The advantage of the autostitching, in addition to time, is that the data generated represent the entire area scanned. Otherwise, one collects data from each quadrant individually.

Data clouds from each individual were initially processed using SolarMap® software (version 5.1.1). This allowed for leveling of the data, using the least squares leveling algorithm, and 'cleaning' of the data, which is the manual removal of microscopic dirt fragments. Microsurface analysis software is sensitive to changes in surface peaks and valleys; it is important for all dirt to be absent from the dataset so that the software does not include them in surface computations. Microfeature confirmation came from observations of detailed representations of surfaces using 2D photosimulations as well as 3D surface reconstructions. Both gave analysts a multitude of views and tremendous flexibility in surface assessment, including the ability to change simulated light direction and angle, to ensure that surface features were limited to legitimate microwear features present. Any surface deemed to have non-masticatory wear, areas obscured by preservative or other taphonomic agents, or that had too much of its surface cleaned (over 10%) were excluded from analysis.

Surface analysis used scale-sensitive fractal geometry

TABLE 1. DENTAL MICROWEAR TEXTURE VALUES FOR INDIVIDUALS EXAMINED IN THIS STUDY.

Specimen	Tooth	Asfc	epLsar	Tfv
Krapina 1	LRM2	1.50993	0.002901	56298.13
Krapina 2	LRM2	1.580163	0.00408	39872.69
Krapina 4	LLM3	1.077937	0.003188	19442.54
Krapina 9	LLM3	0.790417	0.005646	16892.42
Krapina 10	LRM2	1.715061	0.003031	42403.25
Krapina 58	URM2	2.370852	0.003575	39436.88
Krapina 80	LRM2	1.064712	0.00392	50765.3
Krapina 135	ULM2	0.465623	0.002199	35657.62
Krapina 136	ULM1	0.67466	0.003423	39764.1
Krapina 162	URM3	0.214475	0.006651	23127.59
Krapina 164	ULM1	1.586104	0.003738	48927.73
Krapina 165	URM2	0.783699	0.006151	64115.03
Krapina 167	URM1	0.566091	0.005714	16381.35
Krapina 170	URM3	1.544493	0.005081	31714.96
Krapina 172	URM2	0.456676	0.001377	5095.26
Krapina 173	ULM3	0.521748	0.003609	2610.7
Krapina 175	ULM2	1.269073	0.001027	31571.64
Krapina 177	URM2	1.892272	0.007036	19627.84
Krapina 178	URM3	1.276849	0.008537	27800.18
Vindija 11.39	LRM2	0.639923	0.000423	35542.54
Vindija 11.40	LLM1	0.974629	0.003047	50682.29
Vindija 11.45	LLM2	1.075343	0.000435	46854.21
Vindija 12.1	URM2	0.683115	0.007043	52388.02

software, Toothfrax® and Sfrax® (Surfract, www.surfract.com), which computes surface complexity, anisotropy, textural fill volume, scale of maximum complexity, and heterogeneity. For the current study, only the first three are computed. Complexity (Asfc, area-scale fractal complexity) is determined by measuring the change in relative area of the tooth surface when examined at different scales. Surfaces with greater relief are said to be more complex, while surfaces with less relief have lower complexity values. The consumption of hard brittle foods tends to result in higher complexity (e.g., Scott et al. 2012), while softer foods result in low complexity values (e.g., Schmidt et al. 2016). Anisotropy (epLsar) measures the degree to which features on the surfaces are oriented in the same direction. Surfaces dominated by parallel scratches running in the same direction have high anisotropy values. The consumption of tough or fibrous foods will result in high anisotropy values (Scott et al. 2006). Textural fill volume (Tfv) is a measure of the volume of the wear features on the tooth surface (Scott et al. 2006). Teeth with more surface missing will have higher Tfv values.

STATISTICAL ANALYSES AND COMPARISONS

The small sample size from Vindija prevented meaningful statistical testing. Because of the concerns mentioned before regarding inter-machine WLCP data, comparisons to published data are limited to qualitative assessments. For quantitative comparisons, the data herein are compared to data from bioarchaeological specimens, all of which were studied using the Indie machine.

RESULTS

Of the 45 molars examined, 23 molars (19 from Krapina and 4 from Vindija) preserved wear sufficient for data collection (Table 1). Mean Asfc, epLsar, and Tfv values for these specimens are presented in Table 2. Photosimulations and 3D images of microwear on selected specimens are shown in Figure 1. A small sample size from Vindija prevented meaningful statistical testing. Despite the lack statistical analysis, a descriptive analysis of the results still provides valuable insights into diet and environment.

The mean complexity values for both Krapina and Vindija are relatively low (1.12 and 0.84, respectively) com-

TABLE 2. MEAN COMPLEXITY (Asfc), ANISOTROPY (epLsar), AND TEXTURAL FILL VOLUME (Tfv) FOR VINDIJA AND KRAPINA.

		Asfc		epLsar		Tfv	
	N	Mean	SD	Mean	SD	Mean	SD
Krapina	19	1.12	0.58	0.0043	0.002	35,518	14,206
Vindija	4	0.84	0.21	0.0027	0.0031	46,367	7,758

*Although 19 molars were used to calculate Asfc and epLsar for Krapina, only 17 were used to calculate Tfv because two values were outliers.

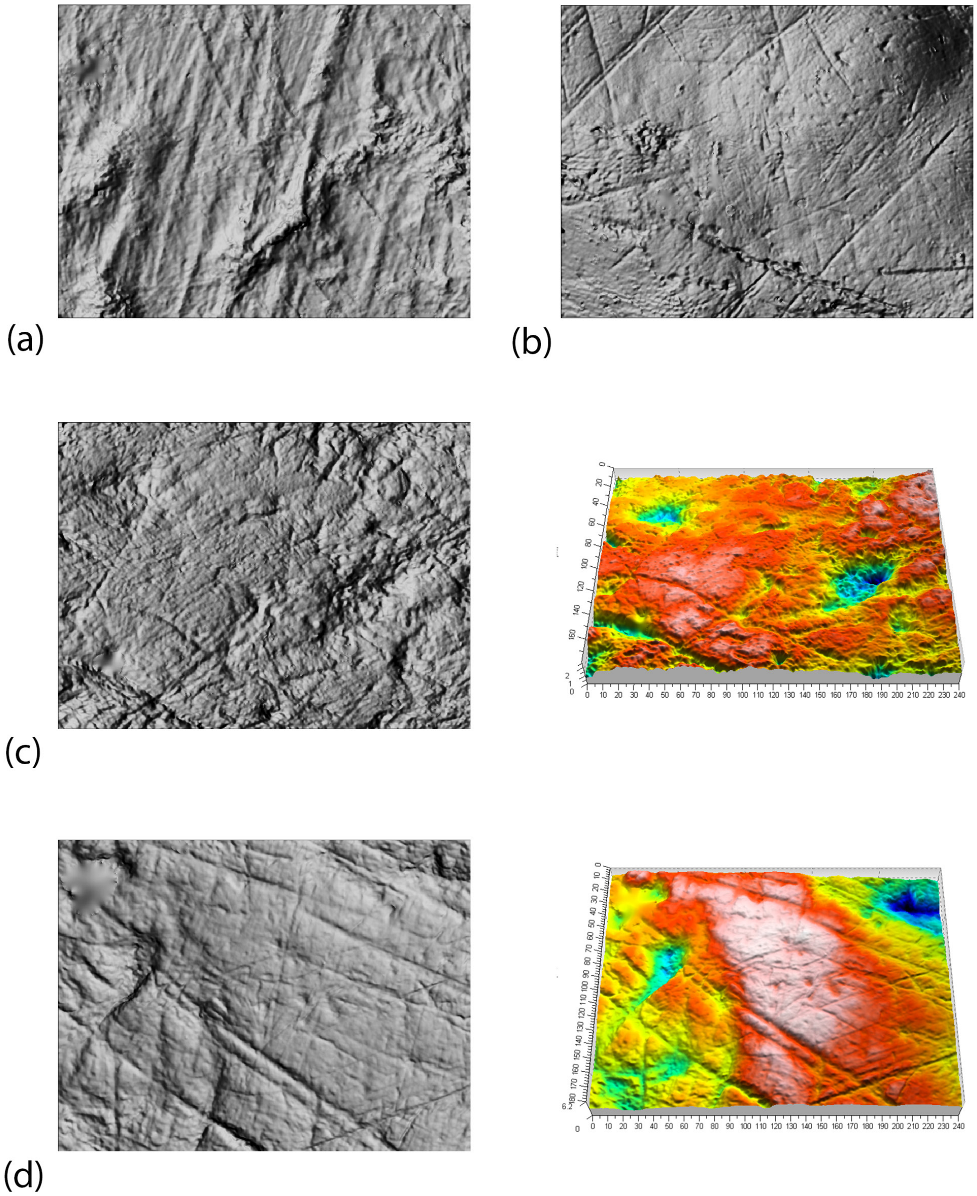

Figure 1. Photosimulations of (a) Krapina 4, (b) Krapina 162, and photosimulations (left) and 3D images (right) of (c) Krapina 173 and (d) Vindija 11.45/Vi 206. (a) Krapina 4 illustrates the anisotropy present in the Krapina sample while (b) Krapina 162 and (c) Krapina 173 exhibited a rougher surface. (d) Vindija 11.45/Vi 206 exhibits both elevated anisotropy and a rough surface that contributed to the higher complexity values for that sample.

TABLE 3. MEAN COMPLEXITY (Asfc) AND ANISOTROPY (epLsar) FOR VINDIJA, KRAPINA, AND COMPARISON GROUPS.

			Asfc		**epLsar**	
	#Subsist	**N**	**Mean**	**SD**	**Mean**	**SD**
Krapina		19	1.12	0.58	0.0043	0.0020
Vindija		4	0.84	0.21	0.0027	0.0031
***Natufian, Israel**	Proto-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	1.20	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

*Schmidt et al. (2016); ^ derived from Chiu et al. (2012); **derived from Frazer (2011)

#Ag=agriculture; Hard food H/G=foragers relying heavily on nuts and seeds; Abrasive food H/G=foragers relying heavily on unprocessed, tough fibrous foods; Past=pastoralism.

pared to modern archaeological samples (e.g., Chiu et al. 2012; Frazer 2011; Mahoney et al. 2016; Schmidt et al. 2016) (Table 3). Vindija has a low mean epLsar (0.0027), but the mean epLsar for Krapina is notably higher (0.0043). Mean Tfv is higher for Vindija (46,367) than for Krapina (35,518).

DISCUSSION

Vindija and Krapina complexity (Asfc) values are similar and near the lower end of the range when compared to Holocene agricultural, hunter/gatherer, and pastoral groups. Mean complexities around 1.0 are found in Middle to Late Archaic foragers from the Eastern Woodlands of the USA as well as Xiongnu and Late Bronze Age/Early Iron Age pastoralists from Mongolia (Frazer 2011; Schmidt et al. 2016). Both of these groups are thought to consume sizable quantities of meat. Values that low also are found in New World farmers thought to have a highly processed diet (Frazer 2011). Most humans, forager and farmer, tend to have complexity values higher than what is seen among the Vindija people, in particular. Recall that meat generates very few dental microwear features (Hua et al. 2015). Since it is unlikely these Neandertals are consuming highly processed domesticates (which can also depress Asfc values), these results suggest they are consuming meat at high levels.

In contrast, the anisotropy values (epLsar) for Vindija and Krapina are dissimilar. Although statistical testing was not possible here, differences of similar magnitude have been found to be significant in other studies with larger sample sizes (e.g., Schmidt et al. 2016). Higher anisotropy values tend to characterize agricultural groups; lower values are more common in foragers. This difference may be related to jaw movement. Farmers tend to eat homogenous diets that lead to a consistent movement of the jaw. Foragers, on the other hand, tend to eat harder foods and a greater variety of foods, both of which lead to jaw move-

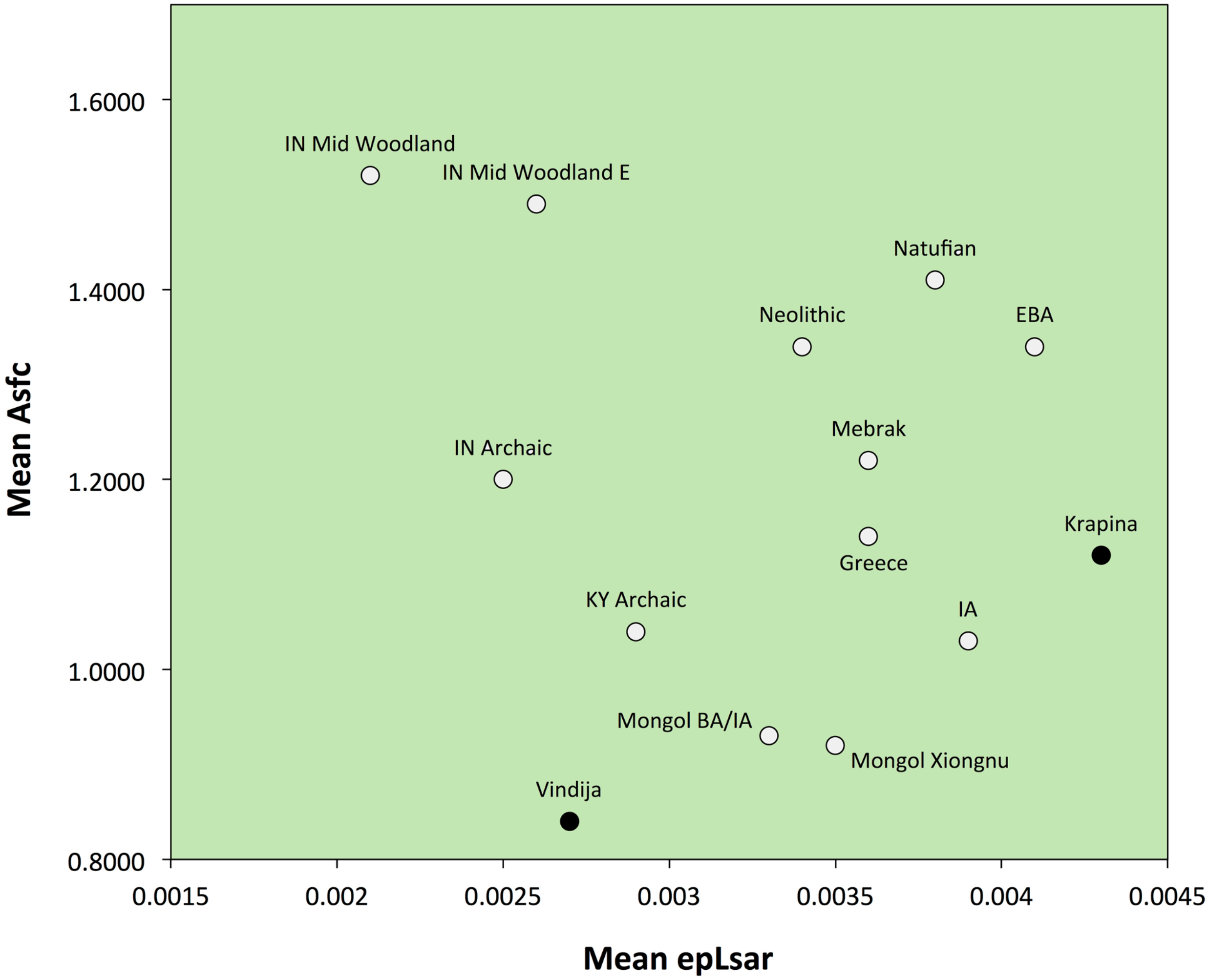

Figure 2. Mean Krapina and Vindija Asfc and epLsar values compared to Holocene humans. Sites are: IN Mid Woodland (Indiana Middle Woodland) and IN Mid Woodland E (Indiana Middle Woodland East), IN Archaic (Indiana Middle to Late Archaic) (source: Frazer 2011); Natufian and Neolithic from Israel (from Chiu et al. 2012); EBA (Early Bronze Age England), LBA (Late Bronze Age England), IA (Iron Age England); Mebrak (~Iron Age, Nepal), Greece (Bronze and Iron Age), Mongol Xiongnu (Xiongnu Period Mongolia), Mongol BA/IA (Bronze Age/Iron Age Mongolia) (source: Schmidt et al. 2016). The Kentucky Archaic data were assembled for this study.

ments in multiple directions. Scores over 0.0035 are found in Mississippian farmers from the Eastern Woodlands of the USA, Early Bronze Age farmers from England, Iron Age farmers from England, and Late Bronze and Iron Age farmers from Greece and Nepal. Populations with values below 0.0030 include Middle and Late Archaic and Middle Woodland foragers from the Eastern Woodlands of the USA (Figure 2). Vindija is below 0.0030 and consistent with foragers. Krapina, however, is over 0.0040, which is above most farmers. Only the people of the Early Bronze Age and Iron Age of England have comparable values. The difference between the two sites may be better understood by considering El Zaatari's data (2010; El Zaatari et al. 2011). She looked at Neandertal DMTA, including that from Vindija, and sought to understand variation via an eco-geographic model. She found harder, less anisotropic diets among woodland Neandertals and softer more anisotropic diets among Steppe Neandertals (El Zaatari, 2007). This difference may be at play here, at least to the extent that it reflects anisotropy. It may be that the Vindija people consumed a diet based more on meat and a variety of plant resources that led to various jaw movements. Krapina, in contrast, may have supplemented its meat diet with plant resources that are more fibrous and tough leading to much greater anisotropy. This supposition may be supported by the textural fill volume data. Vindija has a much higher textural fill volume despite having a lower complexity value than Krapina. This means that the Vindija surfaces were more uneven, a condition commonly found in Holocene foragers.

VINDIJA

The Vindija data indicate a low complexity, low anisotropy, high textural fill volume DMTA profile. Making a broad comparison to the Neandertal record, Vindija is most similar to people of OIS 3 from Central Europe and the Upper Paleolithic modern human sample (El Zaatari 2007), who also have low complexity and low anisotropy values. Overall, the Vindija diet was soft. These results support the stable isotope analyses from Vindija (Richards et al. 2000) indicating a diet high in meat diet. The indication of diverse plant food consumption also may suggest that the environment was different during the time period when the Vindija people inhabited the Zagorje when compared to the presumably warmer, interglacial period (OIS 5e) during which the Krapina people inhabited the same region.

KRAPINA

As with Vindija, the low mean complexity for Krapina suggests that the Neandertals there were consuming few hard, brittle foods. Explaining the anisotropy at Krapina is a challenge since it deviates so noticeably from other foragers. One consideration is the environment. Based on faunal analyses, a variety of environments likely surrounded Krapina. Miracle notes that, "…open forest/parkland with running water would have accommodated most of the animals identified in the Krapina fauna" (Miracle 2007: 214). However, climatic fluctuations throughout the occupation of the site likely occurred making it is difficult to associate specific remains with specific fluctuations. Seasonality can greatly affect food availability and, therefore, diet. Since microwear is a result of food consumed only shortly before death, the season in which an individual dies could affect microwear texture values. As part of a study that examined the correlation between observed dietary behaviors of non-human primates and microwear texture results of the same species, Scott and colleagues (2012) combined data from several sources to determine the percent feeding time by food type for a variety of primates. Different samples of the same species exhibit slight variances in the observed time spent eating specific foods (Scott et al. 2012). It is reasonable to suggest that throughout the year, Neandertals had varied diets as well. Unfortunately, the faunal collections from the sites do not allow a confident assessment of season of death. Therefore, the high anisotropy remains poorly understood.

Data collected by El Zaatari (2007) for modern populations for which ethnographic data were available suggest that sandy or otherwise abrasive particles incorporated into food resources due to preparation or storage techniques has the effect of increasing microwear texture values. Krapina was a sandstone rockshelter, making it plausible that some of those sandy sediments were incorporated into the food the Krapina Neandertals consumed.

As noted previously, foods with different textures will create different kinds of wear. An analysis of the faunal remains from Krapina by Miracle (2007) indicated that *S. kirchbergensis*, or Merck's rhinoceros, is the most abundant species in the faunal collection if the minimum number of individuals (MNI) is used as an indicator of abundance (MNI=23). Markings on these bones suggest processing by Neandertals and likely consumption of significant amounts of Merck's rhinoceros meat. Unfortunately, data on the texture of this meat cannot be gathered since the species is now extinct. However, since meat leaves very little microwear, the consumption of significant amounts of any kind of meat may not be the most appropriate explanation for the high mean epLsar at Krapina. Interestingly, microwear studies of *S. kirchbergensis* indicates that these animals are mixed feeders but lean to the browser end of the mixed feeder scale (van Asperen and Kahlke 2015). However, van Asperen and Kahlke (2015) also note that these "forest rhinoceroses" often included significant grazing in their diet based on local ecological conditions. Thus the presence of *S. kirchbergensis* far from excluded the presence of significant grass resources in the Krapina region.

The higher anisotropy at Krapina indicates the Neandertals there were likely consuming significant quantities of unprocessed fibrous plants that could have included grasses and tubers. In fact, recent research has indicated that hominins ate increasing amounts of C_4 grasses through time. In an examination of carbon isotopes in fossils from the Turkana Basin of Kenya, Cerling and colleagues (2013a) found that fossils attributed to *Homo* had an increased amount of C_4 resources in their diet when compared to the *Australopithecus*/*Paranthropus* specimens from the Turkana Basin. Wynn and colleagues (2013) also found an increase in C_4 resources in *A. afarensis* when compared to *A. anamensis*. However, these trends of increased C_4 plant utilization may vary by region (Sponheimer et al. 2013). Finally, evidence of *Theropithecus* diet indicates an increase in C_4 resources between 1 and 4 million years ago (Cerling et al. 2013b). Interestingly, *Theropithecus* also has high anisotropy values (Scott et al. 2012). Although it is not clear if C_4 grasses were present at the sites in this study, further research to examine whether DMTA values are significantly different in samples that consumed grasses, tubers, or other unprocessed plants, than in samples that consumed few of those resources, will help determine whether the high epLsar values at Krapina can be attributed to consumption of grasses (Henry et al. 2011; 2014).

CONCLUSION

We conclude that the low Asfc values for Vindija and Krapina are consistent with high meat consumers. The high epLsar values at Krapina indicate that the Neandertals there likely consumed significant amounts of unprocessed plants that may have included grasses, tubers, and other fibrous botanical remains. It is less likely they were consuming hard foods like unprocessed seeds or nuts. Thus, although Neandertals and their contemporary anatomically modern humans may have differed in the relative amounts of dietary resources consumed, various analyses, including the present study, indicate that Neandertals did not rely solely on a meat diet.

Our study adds additional information to the growing body of data indicating a complex diet for Neandertals. Furthermore, our study shows the usefulness of DMTA for investigating aspects of dietary intake by Neandertals and demonstrates that use of a single technique to reconstruct Neandertal diet, no matter how reliable that technique may be, is unlikely to provide the entire picture of the dietary resources exploited by these hominins. Although it is likely that early modern humans were perhaps more efficient exploiters of dietary resources available to them during the late Pleistocene, it is clear that Neandertals also exhibit evidence of relatively broad dietary resource exploitation.

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