



Ecogeographic variation in Neandertal dietary habits: Evidence from occlusal molar microwear texture analysis

Sireen El Zaatari^{a,b,*}, Frederick E. Grine^{c,d}, Peter S. Ungar^e, Jean-Jacques Hublin^a

^a Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

^b Wiener Laboratory, American School of Classical Studies at Athens, 54 Soudias Street, 106-76 Athens, Greece

^c Department of Anthropology, Stony Brook University, Stony Brook, NY 11794, USA

^d Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY 11794, USA

^e Department of Anthropology, University of Arkansas, Fayetteville, AR 72701, USA

ARTICLE INFO

Article history:

Received 22 June 2010

Accepted 23 May 2011

Keywords:

Microwear texture analysis

Diet

Neandertal

ABSTRACT

In the late Middle and early Late Pleistocene, Neandertals inhabited a wide variety of ecological zones across western Eurasia during both glacial and interglacial times. To elucidate the still poorly understood effects of climatic change on Neandertal subsistence patterns, this study employs dental microwear texture analysis to reconstruct the diets of Neandertal individuals from various sites across their wide temporal and geographic ranges. The results of this study reveal environmentally-driven differences in the diets of Neandertal groups. Significant differences in microwear signatures, correlated with paleo-ecological conditions, were found among Neandertal groups that lived in open, mixed, and wooded environments. In comparison to recent hunter-gatherer populations with known, yet diverse diets, the occlusal molar microwear signatures of all the Neandertal groups indicate that their diet consisted predominantly of meat. However, the results of this study suggest that plant foods did form an important part of the diet of at least some Neandertal groups (i.e., those that lived in mixed and wooded habitats). Overall, the proportion of plant foods in the Neandertal diet appears to have increased with the increase in tree cover.

© 2011 Elsevier Ltd. All rights reserved.

Introduction

Neandertals are best documented from marine isotope stages (MIS) 6 through 3. Over this long period of time, in which they successfully occupied western Eurasia, Neandertals had to cope with the sometimes harsh and severely changing climatic conditions of the alternating glacial/interglacial cycles of the Middle and Late Pleistocene (e.g., van Andel and Tzedakis, 1996). The fossil and archaeological records indicate that, although their occupation of western Eurasia in the Pleistocene might have been discontinuous (Hublin and Roebroeks, 2009), Neandertals were able to survive in a large variety of environments. Their remains are associated with habitats ranging from warm and forested to cold and open. Changes in vegetation cover in relation to geography and in response to climatic fluctuations must have certainly affected food (plant and animal) availability. Neandertals would have had to adapt to these changes in order to survive. However, the role that these

fluctuations played in their diets is still unclear. Documenting the diet of Neandertals temporally (across the various glacial/interglacial periods) and geographically (across their wide geographic range) is the key to understanding their ability to adapt and survive for such a variable period. A study of Neandertal dietary alteration over time is also essential in determining any evidence of dietary shifts toward the end of their time range, either as a result of the severe climatic fluctuations of MIS 3 (e.g., van Andel, 2002) or possible competition over dietary resources with early modern humans in Eurasia (e.g., Mellars, 2004). For these reasons, this study addresses the effects of environmental changes on Neandertal life through an examination of dietary differences among individuals from different temporal, geographical, and ecological zones using occlusal molar microwear texture analysis.

Neandertal diet studies

Reconstructions of Neandertal diets have been attempted using several techniques including analyses of faunal assemblages (e.g., Binford, 1988; Stiner, 1994; Gaudzinski, 1998; Marean and Kim, 1998; Gaudzinski and Roebroeks, 2000; Munson and Marean,

* Corresponding author.

E-mail address: sireen_elzaatari@eva.mpg.de (S. El Zaatari).

2003), botanic remains (e.g., Madella et al., 2002; Hardy, 2004; Lev et al., 2005), bone and tooth chemistry (Bocherens et al., 1991, 1999, 2001, 2005; Fizet et al., 1995; Richards et al., 2000, 2008; Bocherens and Drucker, 2003; Beauval et al., 2006; Richards and Schmitz, 2008; Richards and Trinkaus, 2009), systemic stress indicators such as dental enamel hypoplasia (e.g., Molnar and Molnar, 1985; Oglivie et al., 1989; Hutchinson et al., 1997; Guatelli-Steinberg et al., 2004), and dental microwear features on incisors (e.g., Ryan, 1993; Krueger et al., 2010) and buccal molar surfaces (Lalueza and Pérez-Pérez, 1993; Lalueza-Fox et al., 1996; Pérez-Pérez et al., 2003).

Although the majority of these studies treated Neandertals as a single group and did not consider possible differences in their diets in relation to different ecogeographic conditions, insights into these possible differences are provided by the results of some of these studies. The stable isotope analyses imply a dietary uniformity among the 15 Neandertal individuals sampled from different European sites (Bocherens et al., 1991, 1999, 2001, 2005; Fizet et al., 1995; Richards et al., 2000, 2008; Bocherens and Drucker, 2003; Beauval et al., 2006; Richards and Schmitz, 2008; Richards and Trinkaus, 2009). These studies suggest that the diets of all these individuals were very similar and consisted almost exclusively of meat from open-ranging, large terrestrial herbivores. It should be noted, however, that these results cannot be considered representative of the overall range of Neandertal diets since all the specimens analyzed are from northern and central European sites and all date to MIS 3, with one exception (dated to MIS 5). Also, analyses of floral remains in site sediments (e.g., Madella et al., 2002; Lev et al., 2005), on tools (e.g., Hardy, 2004), in Neandertal dental calculus (Henry et al., 2010), and possibly in their coprolites (e.g., Callen, 1969), all attest to the contribution of plant foods to the diet of at least some Neandertals.

On the other hand, regional syntheses of zooarchaeological data indicate some level of geographic differences in animal species selection among Neandertal groups. These studies show that Neandertals from northern and central Europe relied mostly on large-bodied herbivores (Conard and Prindiville, 2000; Patou-Mathis, 2000), whereas in southern/Mediterranean Europe there was an increased reliance on medium-sized herbivores (e.g., Boyle, 2000; Aura Tortosa et al., 2002). In addition, evidence for the consumption of small-bodied and aquatic animals has been detected in some Middle Paleolithic sites, mostly in southern/Mediterranean Europe (e.g., Antunes, 2000; Barton, 2000; Finlayson et al., 2001, 2006). These regional syntheses also suggest possible temporal differences in Neandertal diets in response to changes in ecological conditions (Conard and Prindiville, 2000; Patou-Mathis, 2000).

Additional indications for possible changes in Neandertal diets in response to climatic fluctuations have been provided through buccal dental microwear analysis (Pérez-Pérez et al., 2003). The post-canine buccal microwear signatures of various Neandertal specimens show high intra-group variability. The results of this study suggest a link between Neandertal diets and prevailing paleoecological conditions, as indicated by general climatic reconstructions for the marine isotope stages in which they lived. However, as noted by Pérez-Pérez et al. (2003), their classification of Neandertal specimens into broad paleoecological categories based on general conditions of different marine isotope stages does not take geography into account. The geographic differences in climatic conditions within a single stage, as well as the climatic fluctuations in the various sub-phases of a single stage, greatly affected vegetation cover and animal distributions (e.g., van Andel and Tzedakis, 1996).

Although several studies provide some evidence for differences in Neandertal diets through time and space, the role that climatic

changes played is still unclear. Using occlusal molar microwear texture analysis, this study aims specifically to explore this role by examining the differences in Neandertal diet in response to the ecogeographic changes that occurred across their wide temporal and geographic ranges.

Dental microwear analysis

Conventional methods of occlusal dental microwear analysis have proven to be very useful for the reconstruction of diet and tooth use in a variety of animal taxa (e.g., Gordon, 1982; Teaford and O'Leary, 1992; Walker et al., 1994; Ungar, 1996; Daegling and Grine, 1999; MacFadden et al., 1999; El Zaatari et al., 2005). These methods have also proven to be an important tool for inferring the diets of fossil hominins (e.g., Grine, 1986; Grine et al., 2006; Ungar et al., 2006). Occlusal molar microwear analysis has been successfully used to detect slight differences in diets among closely related species and among recent human populations (e.g., Teaford, 1986; El Zaatari, 2008). Microwear analysis has also been shown to have the ability to detect short-term changes in the diet of a single species (e.g., Teaford and Robinson, 1989; Teaford and Oyen, 1989a). This ability is a result of the "Last Supper" phenomenon associated with microwear signatures (Grine, 1986). Because dental microwear signatures are dynamic signatures that have a relatively high turnover rate, they capture, on average, a few days to a few weeks of an individual's diet (Teaford and Oyen, 1989b). Thus, the "Last Supper" phenomenon allows the use of microwear analyses for the examination of species dietary adaptations to different ecological settings (e.g., in the case of species with wide geographical ranges or migratory species), since microwear signatures would generally reflect the diet an individual specimen had a short time before its death, when it would have been in close proximity to the area of its recovery.

Recent advances in the field of dental microwear are further expanding the potential of this technique. Specifically, microwear texture analysis is an automated approach to the study of dental microwear where scanning confocal profilometry replaces scanning electron microscopy, and scale-sensitive fractal analysis is employed in 3-D analysis of microwear features (Ungar et al., 2003; Scott et al., 2005, 2006). It has been shown to be very effective in differentiating archaeological, historical, and prehistoric hunter-gatherer populations that existed in different geographical locations and environmental conditions, and had diverse diets (El Zaatari, 2010). It has also been shown to be able to detect differences in the diets of fossil hominins (Scott et al., 2005; Ungar et al., 2008, 2010). This technique is employed in the current examination of Neandertal diet.

Materials and methods

For the purposes of this study, replicas of the dental remains of 35 adult Neandertal individuals from 23 European and Levantine sites were made following established procedures (Teaford and Oyen, 1989c). Dental specimens were cleaned gently with cotton swabs soaked with water. Acetone, ethyl alcohol, or both were used only when necessary (i.e., when the specimens were covered with preservatives or glue). Impressions were made using President MicroSystem™ (Coltène-Whaledent) (polysiloxane vinyl) impression material and casts were then made with Epo-Tek 301 epoxy resin and hardener (Epoxy Technology).

The dental casts were examined using a Sensofar Plu Confocal Imaging Profiler (Solaris Development, Inc.). Specimens showing post-mortem damage were easily identified and excluded from further study (see El Zaatari, 2010, for details). Dental remains of 25 individuals from 19 sites were found to be well-preserved and free



Figure 1. Map showing the sites included in this study.

of post-mortem taphonomic artifacts (Fig. 1 and Table 1), whereas the teeth of 10 individuals had to be excluded from further analyses due to post-mortem defects. Following Scott et al. (2005, 2006), for the specimens deemed suitable for microwear analysis, four adjoining scans of the crushing/grinding facets (covering a total area of $276 \times 204 \mu\text{m}$) were taken at $100\times$ magnification, with $0.18 \mu\text{m}$ lateral sampling interval and $0.005 \mu\text{m}$ vertical resolution. Using Solarmap Universal software (Solarius Development, Inc.), scans were then leveled, small defects were erased, and photo-stimulations and 3-D images were generated.

Dental microwear data were collected from a total of 25 permanent molars. One molar (either M1 or M2) was selected to represent each individual. The lack of significant differences in microwear patterns between M1 and M2 in recent hunter-gatherer groups makes it acceptable to include data from either of these teeth for the Neanderthal specimens (El Zaatari, 2010). The resulting data were analyzed in Toothfrax and SFrax software (Surfract) using scale-sensitive fractal analysis following. The resulting data were analyzed in Toothfrax and SFrax software (Surfract) using scale-sensitive fractal analysis following Scott et al. (2005, 2006). Scale-sensitive fractal analysis follows principles of fractal geometry (i.e., the appearances of surfaces differ with the scale of observation). Five variables were considered and are described briefly below. Detailed descriptions of these variables and their computations can be found in Scott et al. (2006), Ungar et al. (2007), and El Zaatari (2010).

Complexity ($Asfc$ or area-scale fractal complexity) is a reflection of the change in surface roughness across different scales of observation. It is calculated as the steepest slope of the curve fitted to a plot of relative area versus scale over an order of magnitude. A more complex surface (with a high $Asfc$ value) would be dominated by many overlying features of varying sizes. Anisotropy ($epLsar$ or exact proportion length-scale anisotropy of relief) reflects the orientation of wear features. It is measured as the mean vector of relative lengths (i.e., the sums of line segments divided by straight-line distances between the endpoints) of the sampled profiles across a surface at specific scale ($1.8 \mu\text{m}$) and orientation intervals (5°). A surface dominated by parallel striations would be more anisotropic. The scale of maximum complexity (Smc) measures the fine-scale limit of the steepest part of the curve over which $Asfc$ is calculated. A surface with a high Smc value would be dominated by large features. Texture fill volume (Tfv) reflects the geometrical shape and depth of wear features. It is calculated as the

difference in summed volume of fine and large cuboids (with $2 \mu\text{m}$ and $10 \mu\text{m}$ diameters, respectively) that would fill a surface. A surface with a high Tfv value would have many large and/or deep features. Median values for $Asfc$, $epLsar$, Smc , and Tfv were calculated from the four scans to produce a single value for each variable for each tooth, and therefore, each individual. The fifth variable, heterogeneity ($HAsfc$ or heterogeneity of area-scale fractal complexity), reflects complexity variability across the surface. It is measured as the median absolute deviation of $Asfc$ divided by the median of $Asfc$ for the four scans representing each individual specimen. The individual $HAsfc$ values used in this study were calculated using the four scans for each specimen without splitting single scans into smaller sub-regions. A more heterogeneous surface (with a high $HAsfc$) would have high degree of variability in surface texture.

For the purpose of statistical analyses, each Neanderthal individual was assigned to a temporal, a geographic, and a paleoecological category (Table 1). Temporal categories were based on the marine isotope stage to which the Neanderthal individuals belonged. This broad ranking was necessary because absolute dates are not available for all of the specimens and in some cases, even when available, the ranges of error are so wide as to preclude the placement of all individuals in accurate chronological order. Four temporal categories were used representing MIS 6–3. Geographic categories were based on the latitude of site location. Four geographic categories were specified representing northern, central, and southern/Mediterranean Europe, and the Levant. Paleoecological categories were assigned based on available reconstructions of vegetation cover at the time of deposition of the specimens sampled. These reconstructions are based on all available data from the same site and same layers/levels yielding the hominin remains. Three paleoecological categories were used: open (open vegetation dominates the landscape), mixed (a landscape with a mix of both open and arboreal vegetation elements), and wooded (arboreal vegetation is dominant over open vegetation). Detailed discussions of the assignment of the Neanderthal specimens to these paleoecological categories are available in the SOM.

It should be acknowledged that the three paleoecological categories used in this study are relatively broad, and each of them could potentially encompass a wide range of habitats, which might have offered different food options, especially plant foods (e.g., Hardy, 2010), for the Neanderthals. Yet, it should be noted that

Table 1

List of Neandertal specimens sampled in this study. The marine isotope stages (MIS) are inferred from the dates (absolute or relative) available for each specimen. The vegetation cover information listed represents prevailing conditions during the time of deposition of the hominin remains. Reconstructions are based on paleoenvironmental data available from sedimentary analyses, and floral and/or faunal (both microfaunal and macrofaunal) remains from the same layers/levels of the hominins. In cases where such direct data is not available, it is substituted with data from regional reconstructions (these cases are noted). Vegetation cover is described in three major categories: (1) wooded, when the vegetation in the area is dominated by trees; (2) mixed, when the vegetation is a mix of open and wooded; and (3) open, where trees are very few (generally <10%). Detailed discussions of the assignment of the Neandertal specimens to these paleoecological categories are available in the SOM. Additional individuals (La Ferrassie 1, Marillac, Kulna 1, Arcy II, Monsempron 2, Guattari 2, Vindija 11.40a and 11.39, Grotta Breuil 3, Sidrón 2) were examined but were not found to preserve good microwear and therefore not included in this study.

Site	Specimen	MIS	Paleovegetation Cover
Northern Europe			
Spy	I	3 (Semal et al., 2009)	Open – Faunal data (Cordy, 1988)
Central Europe			
Saint-Césaire	1	3 (Mercier et al., 1991)	Mixed – Faunal data (Marquet, 1988, 1993; Lavaud-Girard, 1993; Patou-Mathis, 1993; Morin, 2004); Pollen data (Leroyer and Leroi-Gourhan, 1993); Sedimentary data (Miskovsky and Lévêque, 1993)
Vindija	11.45 ^a 11.46 12.1	3 (Wild et al., 2001)	Mixed – Faunal data (Miracle et al., 2010)
Ochoz	1	3 or 5 (Schwartz and Tattersall, 2002)	Unavailable ^b
Petit-Puymoyen	2 4	3 (Dupont and Vandermeersch, 1961–1962)	Mixed – Faunal data (Bœuf, 1969)
La Quina	5 20	4 or 3 (Mercier and Valladas, 1998) 4 (Mercier and Valladas, 1998)	Open – Faunal data (Bouchud, 1966; Henri-Martin, 1966)
Subalyuk	1	4 (Schwartz and Tattersall, 2002)	Open – Faunal data (Gross, 1956; Kordos in Schwartz and Tattersall, 2002)
Monsempron	3	5 (Vallois, 1952)	Unavailable ^b
Grotte de l'Hyène (Arcy-sur-Cure)	IVb6 B9	5b (Leroi-Gourhan, 1988)	Open – Sedimentary data (Leroi-Gourhan, 1988)
Rochelot	1098	5d–a (Tournepiche and Couture, 1999)	Mixed – Faunal data (Tournepiche and Couture, 1999)
La Chaise BD	8	6 (Blackwell et al., 1983)	Mixed – Pollen data (Fellag, 1996)
Southern/Mediterranean Europe			
Zafarraya	4	3 (Hublin et al., 1995)	Wooded – Faunal, sedimentological, and pollen data (Barroso Ruiz et al., 2006)
Grotta Breuil	2	3 (Schwarcz et al., 1990–1991)	Wooded – Faunal data (Kotsakis, 1990–1991; Stiner, 1994; Recchi, 1995)
El Sidrón	SDR-005 ^c	3 (Lalueza-Fox et al., 2005)	Wooded – Pollen data (Fortea et al., 2003)
Guattari	3	4 (Grün and Stringer, 1991; Schwarcz et al., 1991)	Unavailable ^d
Saccopastore	1 2	5e–c ^e (Bruner and Manzi, 2008)	Unavailable ^e
Levant			
Amud	I	3 (Valladas et al., 1999; Rink et al., 2001)	Wooded – Faunal data (Rabinovich and Hovers, 2004; Kolska Horwitz and Hongo, 2006; Belmaker and Hovers, 2008)
Kebara	2	4 (Valladas et al., 1987)	Mixed – Faunal data (Eisenmann, 1992; Speth and Tchernov, 1998, 2001, 2002)
Tabun	I II	Unavailable ^f C: 6–5 transition (Grün and Stringer, 2000; Mercier and Valladas, 2003)	Unavailable ^f Mixed – Faunal date (Jelinek et al., 1973)

^a The numbering of the Vindija specimens follows the new numbering system developed in the late 1990s (see Ahern et al., 2004, for details). Following the old numbering system (Wolpoff et al., 1981), the three specimens used here are Vi 231 (specimen 11.45), Vi 259 (specimen 11.46), and Vi 229 (specimen 12.1).

^b No precise paleoclimatic data is available from the sites of Ochoz and Monsempron 3 from interglacial conditions (MIS 5). Climate and vegetation cover varied significantly during MIS 3 and the sub-stages of MIS 5, thus without more reliable dates, it is not possible to correlate the stratigraphy of the sites with regional vegetation reconstructions.

^c This specimen is El Sidrón mandible 1.

^d No paleoecological data is available from the context of Guattari 3, which was recovered from the breccia at the cave entrance (Sergi and Ascenzi, 1955). The Guattari 3 mandible is considered to be older than Guattari 1 and 2 (Grün and Stringer, 1991).

^e The two Saccopastore individuals analyzed here are dated by faunal association to a period between MIS 5e–5c (130–100 ka BP) (Caloi et al., 1998; Bruner and Manzi, 2008). Due to the lack of more specific dates for the Saccopastore remains, vegetation cover reconstructions are not possible. For the site of Saccopastore, during the cold phases of MIS 5 (5d and 5b), open-steppe and grassland vegetation dominated with a low percentage of trees (mostly coniferous trees), whereas during the warmer sub-stages of MIS 5 (5c and 5a), the area was covered by deciduous and Mediterranean woodlands (Follieri et al., 1998).

^f It is still unclear if Tabun I derives from layer C (the same layer as Tabun II) or from layer B, which is higher up in the stratigraphic sequence (Garrod and Bate, 1937; Schwarcz et al., 1998; Bar-Yosef and Callander, 1999; Alpers et al., 2000). Absolute dates place Tabun B within MIS 5, and, more specifically, from sometime toward the end of MIS 5e to 5c (Grün and Stringer, 2000; Mercier and Valladas, 2003). Because of this uncertainty in the stratigraphic location of Tabun I, it cannot be assigned to any of the paleoecological categories identified in this study.

paleoecological reconstructions show that all the specimens attributed to the open category in this study lived under similar ecological conditions in an open, cold-steppe environment. In addition, all the specimens attributed to the wooded category lived in woodlands that developed in warm climates and sustained deciduous and Mediterranean taxa. Indeed, the pollen spectra from the sites of Zafarraya and El Sidrón indicate that deciduous trees

were the dominant trees at the time of Neandertal habitation (Barroso Ruiz et al., 1984, 2006; Fortea et al., 2003) and the microfaunal assemblages in association with Amud 1 indicate a Mediterranean woodland (Belmaker and Hovers, 2008). Only the mixed category includes individuals that were living in areas from a wide range of ecological zones with a mix of both open and wooded vegetation. This category consists of specimens from sites

in the Levant and central Europe. Arboreal taxa from the Levantine sites would have been dominated by warm-loving species. The central European sites can be divided into two groups, the western and the eastern sites. The arboreal taxa of the western sites would have been dominated by coniferous and/or deciduous trees, as is indicated by the pollen spectrum from Saint-Césaire (Leroyer and Leroi-Gourhan, 1993) and La Chaise Bourgeois-Delaunay (Fellag, 1996). The Neandertals from the eastern site of Vindija were living in habitats consisting of a mix of open vegetation and evergreen taiga/montane forest and temperate woodland taxa (Huntley and Allen, 2003). Ideally, an attempt would be made to follow more detailed vegetation reconstructions for the mixed category, yet, because this would simply entail more speculation and reduces sample size in each group, individuals living in different kinds of mixed habitats were grouped together in one category.

Statistical analyses were used first to assess whether or not the microwear signatures of the Neandertals varied in relation to time, geographic location, and paleoecological conditions. Non-parametric correlation tests (Spearman's rho and Kendall's tau) were used to compare the microwear variables for the Neandertal individuals against temporal, geographic, and paleoecological rankings. These rankings were based on the categories identified above, i.e., four temporal ranks (MIS 6 = rank 1, MIS 3 = rank 4), four geographic ranks (northern Europe = rank 1, the Levant = rank 4), and three paleoecological ranks (open = rank 1, wooded = rank 3).

The second set of statistical analyses focused on assessing differences in the five variables among Neandertal populations when the individuals were grouped based on their temporal, geographic, and paleoecological zones. For this purpose, data were rank-transformed before analysis to reduce the possible effects of violating assumptions associated with parametric statistical tests (Conover and Iman, 1981). Data for the five variables were compared among the different groups using a multivariate analysis of variance model (MANOVA) (Neff and Marcus, 1980). Single classification ANOVAs on each variable, along with multiple comparisons tests, were used to determine sources of significant differences when present (Sokal and Rohlf, 1995). Both Fisher's least significant difference (LSD) and Tukey's honestly significant difference (HSD) *post-hoc* tests were used to balance Type I and II errors (Cook and Farewell, 1996).

In the cases where specific temporal and/or paleoecological data were missing for a specific individual, this specimen was excluded from the corresponding statistical analyses. Thus, Ochoz 1 and Tabun I were excluded from the analyses when Neandertal specimens were grouped by marine isotope stages, and Ochoz 1, Monsempron 3, Guattari 3, Saccopastore 1 and 2, and Tabun I were excluded from the analyses when specimens were grouped by paleoecological categories, due to their uncertain dating and/or stratigraphic position.

Finally, a third set of analyses focused on comparing the occlusal microwear texture data of Neandertals to those of four recent hunter-gatherer groups (Tigara, Khoe-San, Chumash, and Fuegians) with known but diverse diets. Differences in microwear signatures of these groups reflecting differences in their diets and food preparation techniques have been documented (see El Zaatari, 2010, for details). For comparisons between the fossils and recent groups, hierarchical cluster analysis, using Euclidean distance and complete linkage (Fortelius and Solounias, 2000), was conducted on the samples that were significantly differentiated by the MANOVA model. Only the variables that showed significant differences among the Neandertal groups in the ANOVA models were used. Standardization using z-scores was first applied to the values to correct for different scales of measurement for the different variables included in the cluster analysis. Neandertal

specimens that could not be included in the fossil groupings due to unavailable information were considered separately.

Results

Raw data for each of the Neandertal individuals, and summary statistics for the Neandertal groups by temporal, geographic, and paleoecological categories are presented in Table 2. Representative micrographs of the Neandertal individuals are illustrated in Fig. 2. The small sample sizes for some of the fossil categories should be noted and should be kept in mind in the interpretation of the results.

Correlations by temporal, geographic, and paleoecological ranks

The results of Spearman's rho and Kendall's tau correlation tests indicate that there is no correlation between time, as represented by the marine isotope stages, and any of the five microwear variables (Table 3). Thus, no specific temporal trend of dietary change was detected for those Neandertals examined. Only one microwear variable, heterogeneity (*HAsfc*), shows significant correlation ($p < 0.05$) with geographic location, such that a trend of increase in heterogeneity values is evident with the decrease in site latitude, i.e., from north to south (Tables 2B and 3). A significant correlation occurs between paleoecological rank and surface complexity (*Asfc*) and between paleoecological rank and heterogeneity (*HAsfc*) ($p < 0.01$ and $p < 0.05$, respectively). Both surface complexity and heterogeneity increase with the increase in tree cover (Tables 2B and 3).

Comparisons by temporal, geographic, and paleoecological categories

The MANOVA results indicate no significant differences in the model among the Neandertal samples when the specimens are grouped by temporal or geographic categories (Tables 2B and 4). However, the MANOVA results detect significant variation among the Neandertal samples when the specimens are grouped by paleoecological categories (Tables 2B and 4). Individual ANOVAs show significant variation in surface complexity (*Asfc*) ($p < 0.05$) as well as heterogeneity (*HAsfc*) ($p < 0.05$) (Table 5A). No significant variation was found for anisotropy (*epLsar*), texture fill volume (*Tfv*), or scale of maximum complexity (*Smc*). *Post-hoc* tests indicate that Neandertals from wooded environments have, on average, significantly greater surface complexity (*Asfc*) compared to those that lived in mixed and open environments (Tables 2B and 5B). Significant variation in mean heterogeneity (*HAsfc*) values was also detected, with Neandertals in open habitats exhibiting lower average heterogeneity than those from mixed and wooded habitats (Tables 2B and 5B).

Comparisons between the recent hunter-gatherer and fossil groups

Means and standard deviations for the microwear variables for four recent hunter-gatherer groups, the Fuegians, Chumash, Khoe-San, and Tigara, are presented in Table 6. The Fuegians included in this study lived in open shrub-tundra vegetation and had a diet consisting almost exclusively of meat, with plant foods forming <15% of the total diet (e.g., Bridges, 1885; Murdock, 1962). The Chumash sample consists of individuals that lived in a Mediterranean-like climate of the island of Santa Cruz and whose diet was predominantly based on fish and marine mammals, in addition to some terrestrial animals and several kinds of plants available on the island (e.g., Timbrook, 1993; Walker, 1996). Ethnographic data indicates that plants formed 36–45% of the diet of the mainland Chumash groups (Murdock, 1964). However, for the Channel Islands

Table 2
Microwear data on the Neandertals analyzed in this study. (A). Individual data. (B). Averages by temporal, geographic, and paleoecological categories as assigned to individual specimens in Table 1.

A.											
Specimen	Tooth	Surface complexity (<i>Asfc</i>)	Anisotropy (<i>epLsar</i>)	Scale of maximum complexity (<i>Smc</i>)	Texture fill volume (<i>Tfv</i>)	Heterogeneity (<i>HAsfc</i>)					
Spy I	RM ²	1.37	0.0032	0.267	9854.3	0.039					
Saint-Césaire 1	RM ¹	2.33	0.0016	0.208	7687.3	0.435					
Vindija 11.45	LM ₂	0.92	0.0026	0.150	2239.4	0.457					
Vindija 11.46	LM ¹	1.17	0.0030	2.033	10389.0	0.108					
Vindija 12.1	RM ²	1.12	0.0031	0.267	17865.4	0.256					
Ochoz 1	RM ₁	1.09	0.0037	0.342	5752.1	0.018					
Petit-Puymoyen 2	LM ¹	2.07	0.0021	0.150	14457.9	0.223					
Petit-Puymoyen 4	RM ₁	2.02	0.0042	0.267	17486.9	0.145					
La Quina 5	RM ₂	1.18	0.0021	0.342	10312.9	0.171					
La Quina 20	RM ²	1.17	0.0014	0.150	8936.2	0.039					
Subalyuk 1	LM ₂	0.75	0.0030	0.418	11573.9	0.239					
Monsempron 3	RM ¹	3.61	0.0026	0.209	15003.3	0.406					
Grotte de l'Hyène IVb6 B9	RM ₁	0.92	0.0016	0.343	13174.0	0.072					
Rochelot 1098	LM ₂	1.61	0.0051	0.417	9899.9	0.223					
La Chaise BD 8	LM ¹	1.46	0.0024	0.509	15933.1	0.076					
Zafarraya 4	RM ₁	2.11	0.0051	0.150	17594.7	0.300					
Grotta Breuil 2	LM ₁	2.94	0.0016	0.209	15454.3	1.032					
El Sidrón 005	LM ₁	2.69	0.0022	7.628	14225.6	0.213					
Guattari 3	RM ₂	0.70	0.0048	0.267	2234.4	0.170					
Saccopastore 1	LM ²	0.97	0.0043	0.208	8734.8	0.783					
Saccopastore 2	RM ²	1.19	0.0026	10.05	14613.1	0.613					
Amud I	RM ₂	3.07	0.0013	0.150	12118.1	0.982					
Kebara 2	LM ₂	1.55	0.0027	0.150	10043.2	0.453					
Tabun I	RM ¹	2.25	0.0034	0.208	15352.5	0.552					
Tabun II	LM ₂	1.13	0.0029	0.267	3351.0	0.220					
B.											
	<i>n</i>	<i>Asfc</i>		<i>epLsar</i>		<i>Smc</i>		<i>Tfv</i>		<i>HAsfc</i>	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Temporal division ^a											
MIS 3	11	1.98	0.75	0.0027	0.0012	1.044	2.252	12670.3	4846.4	0.381	0.334
MIS 4	4	1.04	0.40	0.0030	0.0014	0.246	0.127	8196.9	4119.5	0.225	0.173
MIS 5	5	1.66	1.13	0.0033	0.0014	2.247	4.367	12285.1	2823.7	0.420	0.287
MIS 6	2	1.29	0.23	0.0027	0.0004	0.388	0.171	9642.0	8896.9	0.148	0.102
Geographic division											
Northern Europe	1	1.37	—	0.0032	—	0.267	—	9854.3	—	0.039	—
Central Europe	14	1.53	0.77	0.0027	0.0010	0.415	0.479	11479.4	4514.5	0.205	0.145
Southern/Mediterranean Europe	6	1.77	0.94	0.0035	0.0015	3.086	4.524	12142.8	5673.1	0.519	0.348
Levant	4	2.00	0.85	0.0026	0.0009	0.194	0.056	10216.2	5071.5	0.551	0.319
Paleoecological division ^b											
Open	5	1.08	0.24	0.0023	0.0079	0.303	0.101	10770.2	1645.9	0.112	0.089
Mixed	10	1.54	0.47	0.0030	0.0010	0.442	0.571	10935.3	5519.6	0.260	0.142
Wooded	4	2.71	0.42	0.0026	0.0018	2.034	3.729	14848.2	2291.4	0.632	0.435

^a La Quina 5, Ochoz 1, and Tabun I were excluded from this analysis due to their uncertain MIS attribution.

^b Ochoz 1, Monsempron 3, Guattari 3, Saccopastore 1 and 2, and Tabun I are excluded from this analysis due to the unavailability of associated paleovegetation information.

inhabitants (including the Santa Cruz Island inhabitants used in this study), the proportion of plants in the diet would have been somewhat lower since the islands had fewer terrestrial resources compared to the mainland (Erlandson et al., 2009). The Khoe-San sample consists of individuals from the site of Oakhurst Shelter, South Africa. They lived in montane forest environment, which was in close proximity to the fynbos environment, and had a diet consisting of substantial amounts of plant foods (e.g., Sealy, 2006). Ethnographic studies show that 60–80% of the traditional diet of San hunter-gatherers consisted of plant food (e.g., Lee, 1979; Silberbauer, 1981). The Tigara sample consists of individuals that were living in the arctic climate of the site of Point Hope, Alaska. Ethnographic data shows that the diet of Alaskan Inuit consisted of mostly meat, with plant foods forming <6% of the diet (Murdoch, 1963). It should be noted that the Tigara ingested large amounts of sand particles that were integrated into their diet as part of their food preparation techniques (de Poncins, 1941; Giddings, 1967). Significant differences in the microwear signatures of these four groups, reflecting the reported differences in their diets, have already been documented and discussed (see El Zaatari, 2010, for details).

Hierarchical cluster analysis was conducted on surface complexity and heterogeneity variables with the Neandertal specimens grouped by paleoecological categories. Only these variables and this grouping were used since these were the only variables and grouping that showed significant differences in the MANOVA and ANOVA models. The results of the cluster analysis show that the Neandertals from open environments cluster closest to the Fuegians and the Neandertals from areas with mixed vegetation cluster closest to the Chumash (Fig. 3). The Neandertals from wooded environments join on a second-order, with a cluster including both the open and mixed habitat Neandertal groups (Fig. 3).

As for the Neandertal individuals with unavailable paleoecological information, Guattari 3 and Ochoz 1 cluster closest to the Neandertals from open vegetation sites and the Fuegians from the recent hunter-gatherer groups (Fig. 3). Tabun I is closest to the Neandertals from wooded environments. The two individuals from Saccopastore (1 and 2) cluster together and are closer to the Neandertals from wooded environments than to the rest of the Neandertal groups, although they are not as close to this group as Tabun I. Monsempron 3 clusters closest to the Khoe-San group.

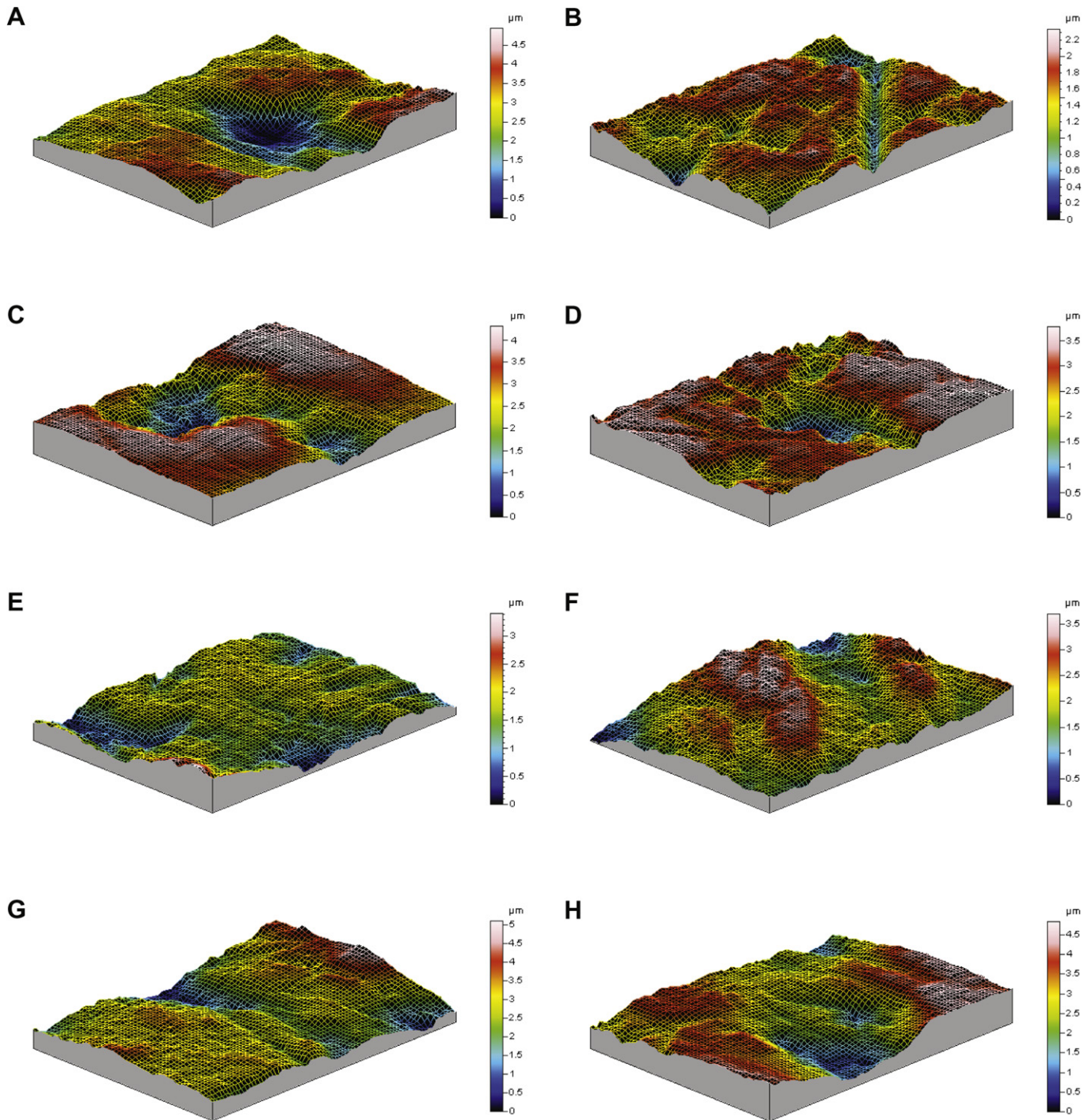


Figure 2. Three-dimensional axiomatic representations of microwear surfaces for several Neandertal individuals: (A) Subalyuk 1; (B) Guattari 3; (C) Kebara 2; (D) Vindija 11.45; (E) Grotta Breuil 2; (F) Zafarraya 1; (G) Monsempron 3; (H) Ochoz 1. Each image represents an area $138 \mu\text{m} \times 104 \mu\text{m}$ on the original tooth surface.

Discussion

The efficacy of microwear texture analysis as a tool for dietary reconstruction has been documented for several species (e.g., Scott et al., 2005, 2006; Ungar et al., 2007, 2008). Of particular relevance to the current study is the demonstration of its ability to distinguish recent hunter-gatherer groups on the basis of their diets and food preparation techniques (El Zaatari, 2010). In particular, El Zaatari (2010) found that the microwear signatures of groups whose diets included large amounts of extraneous abrasive particles

introduced during food preparation (e.g., Tigara) were significantly different from those whose diets did not include such preparatory techniques (i.e., Khoe-San, Chumash, and Fuegians). Moreover, a significant difference was found in microwear fabrics among the Khoe-San, Chumash, and Fuegians, when the groups were ranked by overall level of variety in dietary items and the amount of plant foods in their diet (the Fuegians having the lowest levels for both and the Khoe-San having the highest) (Tables 6 and 7). As demonstrated in Table 7, with the increase in individual dietary variability and the increased addition of plant foods to the diet,

Table 3

Correlation results for microwear variables with temporal, geographic, and paleoecological ranks. Significant correlations ($p < 0.05$) are represented in bold.

	Spearman's rho	p	Kendall's tau	p
Temporal rank (four ranks: MIS 6–3) ^a				
MIS 6: $n = 2$, MIS 5: $n = 5$, MIS 4: $n = 4$, MIS 3: $n = 11$				
Surface Complexity (<i>Asfc</i>)	–0.319	0.148	–0.235	0.168
Anisotropy (<i>epLsar</i>)	0.076	0.738	0.047	0.783
Scale of maximum complexity (<i>Smc</i>)	0.263	0.236	0.193	0.257
Texture fill volume (<i>Tfv</i>)	–0.171	0.448	–0.130	0.444
Heterogeneity (<i>HAsfc</i>)	–0.125	0.579	–0.094	0.581
Geographic rank (four ranks: northern, central, southern/Mediterranean Europe, Levant)				
Northern Europe: $n = 1$, central Europe: $n = 14$, southern/Mediterranean Europe: $n = 6$, Levant: $n = 4$				
Surface Complexity (<i>Asfc</i>)	0.227	0.276	0.177	0.272
Anisotropy (<i>epLsar</i>)	0.041	0.847	0.034	0.834
Scale of maximum complexity (<i>Smc</i>)	–0.268	0.196	–0.202	0.209
Texture fill volume (<i>Tfv</i>)	0.036	0.863	0.025	0.875
Heterogeneity (<i>HAsfc</i>)	0.582	0.002	0.464	0.004
Paleoecological rank (three ranks: open, mixed, wooded) ^b				
Open: $n = 5$, mixed: $n = 10$, wooded: $n = 4$				
Surface Complexity (<i>Asfc</i>)	0.724	0.000	0.612	0.001
Anisotropy (<i>epLsar</i>)	0.029	0.905	0.022	0.907
Scale of maximum complexity (<i>Smc</i>)	–0.127	0.604	–0.102	0.588
Texture fill volume (<i>Tfv</i>)	0.388	0.100	0.277	0.141
Heterogeneity (<i>HAsfc</i>)	0.618	0.005	0.512	0.007

^a La Quina 5, Ochoz 1, and Tabun I were excluded from this analysis due to their uncertain MIS attribution.

^b Ochoz 1, Monsempron 3, Guattari 3, Saccopastore 1 and 2, and Tabun I are excluded from this analysis due to the unavailability of associated paleovegetation information.

there is an increase in surface complexity, texture fill volume, and heterogeneity, and a decrease in average anisotropy and scale of maximum complexity. The documentation of this high correlation between all the microwear variables and diet in recent hunter-gatherer groups justifies the use of microwear texture analysis for the reconstruction and interpretation of the diets of fossil hominins, including Neandertals.

Table 4

MANOVA results by temporal, geographic, and paleoecological divisions. Significant p -values ($p < 0.05$) are represented in bold.

	Value	F	Hypothesis df	Error df	p
Temporal division (four divisions: MIS 6–3) ^a					
MIS 6: $n = 2$, MIS 5: $n = 5$, MIS 4: $n = 4$, MIS 3: $n = 11$					
Wilks' Lambda	0.533	0.639	15.000	39.049	0.825
Pillai's Trace	0.533	0.691	15.000	48.000	0.781
Hotelling's Trace	0.695	0.587	15.000	38.000	0.866
Geographic division (Three divisions: central, southern/Mediterranean Europe, Levant) ^b					
Central Europe: $n = 14$, southern/Mediterranean Europe: $n = 6$, Levant: $n = 4$					
Wilks' Lambda	0.577	1.077	10.000	34.000	0.406
Pillai's Trace	0.467	1.096	10.000	36.000	0.391
Hotelling's Trace	0.658	1.053	10.000	32.000	0.425
Paleoecological division (three ranks: open, mixed, wooded) ^c					
Open: $n = 5$, mixed: $n = 10$, wooded: $n = 4$					
Wilks' Lambda	0.203	2.931	10.000	24.000	0.015
Pillai's Trace	0.932	2.269	10.000	26.000	0.046
Hotelling's Trace	3.269	3.596	10.000	22.000	0.006

^a La Quina 5, Ochoz 1, and Tabun I are excluded from this analysis due to their uncertain MIS attribution.

^b The northern Europe sample is excluded from this analysis because it has one specimen only (Spy I).

^c Ochoz 1, Monsempron 3, Guattari 3, Saccopastore 1 and 2, and Tabun I are excluded from this analysis due to the unavailability of associated paleovegetation information.

Table 5

Individual ANOVAs and *post-hoc* test results for the paleoecological division. Significant p -values ($p < 0.05$) are represented in bold. (A). Individual ANOVAs. (B). Multiple comparison tests (matrices of pairwise mean differences).

A.							
		Sum of Squares	df	Mean Square	F	p	
Surface complexity (<i>Asfc</i>)	Effect	319.650	2	159.825	10.214	0.001	
	Error	250.350	16	15.647			
Anisotropy (<i>epLsar</i>)	Effect	64.675	2	32.338	1.025	0.381	
	Error	504.825	16	31.552			
Scale of maximum complexity (<i>Smc</i>)	Effect	10.350	2	5.175	0.148	0.864	
	Error	559.650	16	34.978			
Texture fill volume (<i>Tfv</i>)	Effect	100.050	2	50.025	1.703	0.214	
	Error	469.950	16	29.372			
Heterogeneity (<i>HAsfc</i>)	Effect	218.850	2	109.425	4.993	0.021	
	Error	350.650	16	21.916			

B.							
		Open		Mixed			
		Value	p	Value	p		
			Tukey's	Fisher's	Tukey's	Fisher's	
Wooded							
<i>Asfc</i>	11.85	0.001	0.000	7.85	0.011	0.004	
<i>HAsfc</i>	9.75	0.018	0.007	4.15	0.318	0.153	
Mixed							
<i>Asfc</i>	4.00	0.187	0.083				
<i>HAsfc</i>	5.60	0.105	0.044				

Neandertal dietary adaptations

Correlations with paleoecological reconstructions The Neandertals were able to adapt to and survive the dramatic climatic fluctuations that western Eurasia witnessed during the late Middle and early Late Pleistocene. Studies of floral and faunal remains from numerous sites in western Eurasia indicate that these climatic changes greatly affected the distributions of plant and animal species, i.e., the food sources for the Neandertals. These studies show that the paleoecology of any one area generally varied between glacial and interglacial times, such that during glacial and stadial times, cold-adapted plant and animal species dominated over warm-loving taxa, while the opposite pattern was seen during interglacial and interstadial times (e.g. van Andel and Tzedakis, 1996). Climatic reconstructions also show that during any single MIS, western Eurasia was divisible into several climatic/paleoecological zones (e.g., van Andel and Tzedakis, 1996). Overall, the areas of southern and Mediterranean Europe were characterized by more continuity in plant and animal records compared to areas further to the north. These northern areas witnessed local extinctions of some plant and animal species, or their retreat to areas with more favorable conditions during cold episodes, while during warm episodes they witnessed colonization by new species and re-colonization from refugia by older community members of plants and animals (Tzedakis and Bennett, 1995). This resulted in the mixing of elements, creating various associations of species, and giving each interglacial period an individual character different from the ones before it (de Jong, 1988).

With the considerable effects the climatic changes had on the animal and plant distributions in western Eurasia, it comes as no surprise that a strong correlation exists between Neandertal microwear variables and the paleoecological conditions (represented here in terms of vegetation cover) of the area in which they lived. The Neandertal specimens in this study can be divided into three major groups: those that lived in open, cold-steppe

Table 6

Microwear data for the recent hunter-gatherer groups (data from El Zaatari, 2010).

	Fuegians	Chumash	Khoe-San	Tigara
Surface Complexity (<i>Asfc</i>)				
Mean	0.948	2.787	3.548	6.569
SD	0.291	2.344	1.601	5.807
Anisotropy (<i>epLsar</i>)				
Mean	0.0044	0.0023	0.0020	0.0029
SD	0.0014	0.0007	0.0010	0.0015
Scale of maximum complexity (<i>Smc</i>)				
Mean	0.400	0.190	0.176	0.213
SD	0.135	0.055	0.051	0.072
Texture fill volume (<i>Tfv</i>)				
Mean	5224.8	6635.9	9272.0	11912.2
SD	3522.5	3191.8	6051.2	4656.7
Heterogeneity (<i>HAsfc</i>)				
Mean	0.109	0.191	0.325	0.267
SD	0.027	0.121	0.208	0.201

vegetation (Spy I, Subalyuk 1, Grotte de l'Hyène IVb6 B9, La Quina 5 and 20), those that inhabited areas with mixed vegetation (Saint-Césaire 1, Vindija 11.45, 11.46, and 12.1, Petit-Puymoyen 2 and 4, Rochelot 1, La Chaise BD 8, Kebara 2, Tabun II), and those that inhabited wooded environments (Zafarraya 1, Grotta Breuil 2, El Sidrón 1, Amud I). The results of this study show that the microwear signatures, and therefore the diets, of the individuals from these three groups differed significantly. Increased tree cover was found to be correlated with an increase in the levels of surface complexity and heterogeneity, likely reflecting increased ingestion of hard items and an increase in the level of individual dietary variability.

Comparison of Neandertal wear fabrics to those of the recent hunter-gatherer groups reveals that none of the Neandertal groups show close similarity to the Tigara (Fig. 3). This suggests that the Neandertal diets likely included fewer abrasives than that of the Tigara. As noted above, the wear fabrics of this recent group are greatly influenced by food preparation techniques. Microwear study provides little evidence for inclusion of such exogenous abrasives in the diets of Neandertals. This observation also suggests that caution should be exercised when using recent hunter-gatherers that inhabited cold climates as analogs for Neandertals; living in similar environments does not always imply similar dietary or behavioral adaptations.

Neandertal specimens that derive from open-steppe environments evince microwear patterns that more closely resemble those of the Fuegians (Fig. 3). The open-steppe conditions in Europe during the cold glacial phases were most likely quite similar to

Table 7

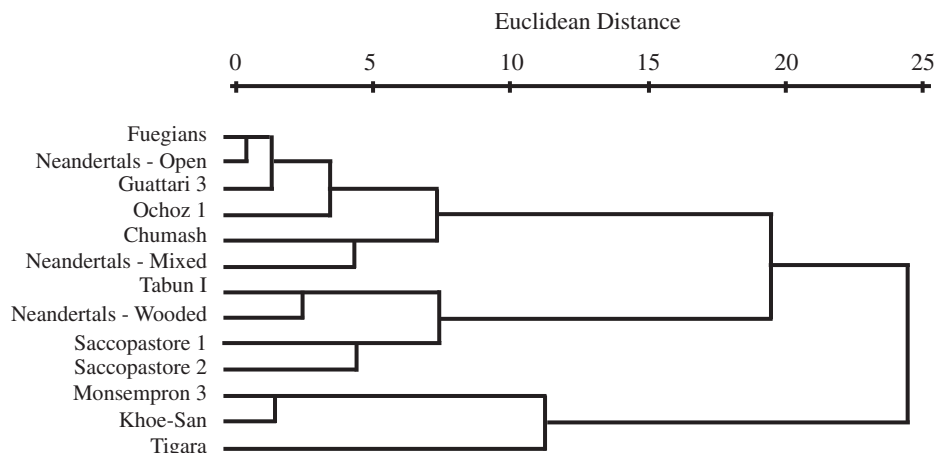
Correlation results for microwear variables with dietary ranks for the recent hunter-gatherer groups: Fuegians (almost exclusively meat diet), Chumash (mostly meat diet), and Khoe-San (mixed diet). Significant correlations ($p < 0.05$) are represented in bold.

	Spearman's rho	<i>p</i>	Kendall's tau	<i>p</i>
Dietary rank (three ranks: almost exclusively meat, mostly meat, mixed diet)				
Almost exclusively meat: $n = 6$, mostly meat: $n = 13$, mixed diet: $n = 9$				
Surface Complexity (<i>Asfc</i>)	0.658	0.000	0.543	0.000
Anisotropy (<i>epLsar</i>)	−0.552	0.002	−0.457	0.003
Scale of maximum complexity (<i>Smc</i>)	−0.601	0.001	−0.527	0.001
Texture fill volume (<i>Tfv</i>)	0.360	0.060	0.303	0.046
Heterogeneity (<i>HAsfc</i>)	0.509	0.006	0.409	0.007

those of Tierra del Fuego today. The sample of Fuegians included here belonged to individuals whose diet relied almost exclusively on meat (e.g., Bridges, 1885; Murdock, 1962). Thus, based on the similarities in their microwear signatures, it is possible to reconstruct the diet of these Neandertals as consisting almost exclusively of meat, with an overall low individual dietary variability.

The Neandertals from mixed environments cluster closest to the Chumash among the recent hunter-gatherer samples (Fig. 3). The Chumash sample consists of individuals that lived in Mediterranean-like climates and had a diet predominantly based on meat in addition to several kinds of plants, including islay, manzanite, mangle berries, tarweed seeds, tubers, and sage (e.g., Timbrook, 1993; Walker, 1996). The similarity in signatures between these Neandertals and the Chumash suggests a diet for the former that consisted largely of meat, but also likely included several kinds of plant foods.

The Neandertals from more wooded environments were found to form a second-order cluster with the recent hunter-gatherers that relied predominantly on meat for their subsistence, i.e., the Fuegians and Chumash. Yet, as indicated by the clustering, the microwear signatures of the wooded habitat Neandertal group do not resemble those of the Fuegians and Chumash as closely as do those of the Neandertal groups from more open habitats (Fig. 3). Indeed, the Neandertals from wooded habitats were found to have higher levels of surface complexity and heterogeneity compared to the other Neandertal groups. This suggests that the Neandertals from wooded environments had more of a mixed diet, probably consisting of higher proportions of plant foods, compared to the Neandertals from more open habitats.

**Figure 3.** Hierarchical Cluster Analysis using Euclidean distance and complete linkage.

Concerning the six additional Neandertal individuals included in this study, but for which paleoecological data are unavailable (Ochoz 1, Monsempron 3, Saccopastore 1 and 2, Guattari 3, and Tabun I), Ochoz 1 and Guattari 3 group with the Neandertals from open environments and the Fuegians. Ochoz 1 is of uncertain date and there is no clear indication of the vegetation cover from the associated finds. The cave of Guattari provided three Neandertal fossils. The Guattari 3 mandible included in this study was recovered from the breccia at the cave entrance (Sergi and Ascenzi, 1955). This mandible is considered to be older than the Guattari 1 and 2 remains (Grün and Stringer, 1991). Absolute dates of several levels of the cave bracket the Guattari 3 mandible to between 74 ka and 60 ka (Grün and Stringer, 1991; Schwarcz et al., 1991). This date places it well within MIS 4. No paleoecological data is available from the context of Guattari 3. But, based on regional pollen sequences, MIS 4 vegetation was dominated by grassland and steppe formations with few weak expansions of trees (Follieri et al., 1998). van Andel and Tzedakis (1996) also reconstructed the vegetation of the area of the Guattari Cave during the middle of MIS 4 as generally an arid cold-steppe. This would be in accord with the results of the microwear analysis.

The dating of the two Saccopastore individuals analyzed here is uncertain. They have been attributed to MIS 5e (Segre, 1983); however, faunal associations indicate that these remains might in fact be a bit younger than MIS 5e and might date to the later sub-stages of MIS 5, somewhere between MIS 5e and 5c (e.g., Caloi et al., 1998; Bruner and Manzi, 2008). For the site of Saccopastore, during the warmer sub-stages of MIS 5 (5c and 5a), the area was covered by deciduous and Mediterranean woodlands, while during the colder phases of MIS 5 (5d and 5b), open-steppe and grassland vegetation would have dominated, with a relatively low percentage of trees consisting mostly of coniferous plants (Follieri et al., 1998). The two Saccopastore specimens cluster together, and fall closest to the Neandertals from wooded environments (Fig. 3). This suggests that they likely lived in somewhat wooded environments, with conditions more similar to those that would have prevailed during the warmer sub-stages of MIS 5 (5c or 5a).

The stratigraphic position of Tabun I remains uncertain. It is unclear whether it derives from layer C (the same layer as Tabun II), which is dated to the MIS 6–5 transition, or from the younger layer B, which is dated to within MIS 5e or the beginning of MIS 5c (Garrod and Bate, 1937; Schwarcz et al., 1998; Bar-Yosef and Callander, 1999; Alpers et al., 2000; Grün and Stringer, 2000). During the time of deposition of Tabun layer C, the Levant was covered with a mix of open and wooded vegetation (Jelinek et al., 1973), whereas during the deposition of Tabun layer B, the area was probably covered with more wooded vegetation (Cheddadi and Rossignol-Strick, 1995). The clustering of Tabun I with Neandertals from wooded environments rather than with those from mixed environments – to which Tabun II belongs – might suggest that the Tabun I specimen lived under more wooded conditions than Tabun II. This, in turn, might be taken as corroborative evidence that they derive from different levels in the site.

The microwear signature of Monsempron 3 places it away from all the other Neandertals studied and aligns it with the Khoe-San from the recent hunter-gatherers (Fig. 3). This indicates that the diet of the Monsempron 3 Neandertal consisted of a higher proportion of plants compared to the other Neandertals analyzed. It might be the case that Monsempron 3 was living in a warm sub-stage of MIS 5 when a greater variety of plant food items was available.

Overall, the clustering of all the Neandertals, with the exception of Monsempron, with the Fuegians and Chumash rather than the Khoe-San shows that their microwear patterns are consistent with a diet relying predominantly on meat. Nevertheless, the results of this study indicate that plant foods also likely formed an important

part of the diet of many Neandertals, as reflected by the clustering of many specimens away from the Fuegians, and instead, either closely clustering with the Chumash or forming a second-order clustering to these two recent populations. Yet, microwear data suggest that Neandertal consumption of plant foods remained generally lower than the Khoe-San group.

Correlation with geographic location The microwear data suggest an increase in Neandertal dietary diversity with a decrease in their habitat latitude, i.e., from northern Europe to the Levant. Studies of faunal remains also indicate greater diversity in the diets of southern European Neandertals compared to their conspecifics from northern and central Europe (e.g., Stiner, 1994; Antunes, 2000; Barton, 2000; Finlayson et al., 2001, 2006). However, it should be noted that the correlation between microwear and geography might be an effect of a bias in the Neandertal samples from southern/Mediterranean Europe and the Levant toward specimens that derive largely from wooded environments, whereas the samples from northern and central Europe consist largely of individuals from regions of open and mixed vegetation. Thus, the correlation between microwear and geographic location might rather reflect an underlying relationship with paleoecological categories (as determined based on both geographic location and marine isotope stage) rather than geographic location alone.

Correlations with time This study failed to detect any specific trend in Neandertal dietary change through time. This is perhaps expected because climate (and food sources) did not change in a consistent manner toward either cold or warm conditions, but rather alternated between cold and warm phases from MIS 6 to 3.

Implications for Neandertal behavior

Neandertals have been regarded, on the basis of carbon and nitrogen stable isotope analyses from nine northern and central European sites, as top-level carnivores feeding mostly on terrestrial herbivores (Bocherens et al., 1991, 1999, 2001, 2005; Fizet et al., 1995; Richards et al., 2000, 2008; Bocherens and Drucker, 2003; Beauval et al., 2006; Richards and Schmitz, 2008; Richards and Trinkaus, 2009). The dental microwear data are generally in agreement with the results of the stable isotope analysis in classifying the Neandertals, including those from northern and central European sites (that form the majority of the open and mixed dietary categories specified in this study) as largely carnivorous, and closely resembling recent humans that consumed mostly meat (i.e., the Fuegians and the Chumash). Yet, unlike the results of stable isotope analyses to date, the microwear data may differentiate samples at a finer scale. Eight of the nine Neandertals that have been analyzed for stable isotopes date to MIS 3, and vegetation reconstructions indicate open cold-steppe (e.g., Spy) (Bocherens et al., 2001) and mixed environments (e.g., Vindija) (Miracle et al., 2010). Although no distinction was found in their stable isotope signatures, microwear data suggest subtle differences, such that the microwear patterns of the Neandertals from open cold-steppe environments were found to most closely resemble those of modern Fuegians, and the patterns of the Neandertals from mixed environments were found to be most similar to those of the Chumash. It should also be noted that the results of the microwear analyses show that for at least some Neandertal groups, specifically those from mixed and wooded habitats, plant foods formed an important part of the diet. However, since none of the Neandertal groups clustered close to the Khoe-San, it appears that the proportion of plant foods in the diets of all the Neandertal specimens (with the exception of Monsempron) was lower than that of meat.

The results of this study also suggest that Neandertals from wooded environments (the majority of the southern/Mediterranean Europe and Levantine individuals analyzed in this study) had

a more varied diet than those from more open environments (the majority of the central and northern European sample). The Neandertals from wooded environments exhibit microwear signatures indicative of an even more catholic diet compared to the Neandertals from open and mixed habitats. Unfortunately, stable isotope data are unavailable for Neandertal specimens from southern latitudes (or wooded environments).

The significant differences in microwear among the Neandertals that lived in different paleoecological conditions attest to their dietary flexibility and their ability to adapt to changes in food resources. With an increase in tree cover, there was a concomitant increase in overall dietary variability and consumption of hard items. Moreover, Neandertal microwear signatures reflect high levels of habitat specificity on two levels. First, at the site level, the similarity of surface complexity values for individuals from the same sites (i.e., La Quina, Petit-Puymoyen, Vindija, Saccopastore) reflect similarity in food items consumed. On a larger scale, the results of this study show that individuals from similar paleoecological conditions most likely ate items with similar fracture properties.

The lack of significant differences in microwear signatures among the Neandertal samples when the individuals were grouped based on either geographic ranks or temporal ranks alone, indicates that the Neandertals, from their wide geographic and temporal ranges, may have had similar dietary adaptations to climatic changes, at least in attributes reflected in microwear texture patterns. Of particular interest in this respect is the comparison of the diets of Neandertals from MIS 3 to earlier individuals, the potential of this research to shed light on the behavior of Neandertals who lived during the last part of their time range as well as on the possible effects of both the severe and short-lived climatic fluctuations of MIS 3, and the possible effect that the arrival of modern humans on the landscape might have had on Neandertal behavior.

The lack of any distinction in the microwear signature of the MIS 3 Neandertals as a group ($n = 11$) from the earlier three groups (MIS 6, 5, and 4) suggests that the diets of Neandertals dated to the later part of their time range were not significantly different from those who existed during the earlier periods of MIS 6–4 (see Table 4). In addition, the microwear data do not indicate any particular dietary features for the late surviving Neandertals (i.e., Spy, Saint-Césaire, Zafarraya, Breuil, and Vindija) that could not be explained by the correlation between diet and the paleoecological conditions observed in Neandertals from earlier periods. Indeed, differences in the diets of the five last surviving Neandertals included in this study follow the expected pattern seen in the earlier Neandertals, such that, those from wooded environments (i.e., Zafarraya and Breuil) were suggested to have a more catholic diet compared to the specimens from more open environments (i.e., Spy, La Quina, Saint-Césaire, Vindija). These results suggest that the MIS 3 Neandertals, at least those included in this study, were able to cope with the severe climatic fluctuations of this stage through changing their diets in much the same way Neandertals from earlier periods did. The continued flexibility in diets of Neandertals throughout their time range, including MIS 3, does not appear to support a link between the severe climatic fluctuations during MIS 3 and the extinction of the Neandertals due to their inability to adapt their diet to these fluctuations.

Concerning any possible competition over resources with modern humans as a cause for the disappearance of the Neandertals, again, the results of this study do not show any special or unexpected shifts in the diets of the late surviving Neandertals. It should be noted, however, that the individuals analyzed here might not represent the diet of Neandertals from the very end of their time range, since the latest surviving specimens included in this study are dated to 36–33 ka (e.g., Mercier et al., 1991; Hublin et al., 1995; Semal et al., 2009), whereas there is evidence that Neandertals most likely

survived for additional few thousands of years (Finlayson et al., 2001). Also, even with the latest known Neandertals, there is still no clear evidence that they lived in close geographic proximity to (or “competed” directly with) any modern human groups.

Conclusions

Through the analysis of occlusal molar microwear signatures of 25 adult individuals from 19 western Eurasian sites, this study examined the effects of climatic change on the diets of Neandertal groups across both their temporal and geographical ranges. The results of this study reveal significant correlations between microwear fabrics, specifically surface complexity and heterogeneity, and paleoecological conditions. Significant differences in microwear textures among Neandertals that inhabited open, mixed, and wooded environments were detected. The microwear fabrics of Neandertals that inhabited open environments were found to exhibit lower levels of surface complexity and heterogeneity than those that lived in mixed and wooded habitats, suggesting lower consumption of hard items and a higher level of individual dietary homogeneity for the former. Also, Neandertals that inhabited areas with a mixed vegetation were found to have lower complexity values than those from wooded environs.

In comparison to recent hunter-gatherer groups, the wear of the majority of Neandertal specimens appears to be most similar to recent people whose diets consisted mostly of meat (i.e., the Fuegians and Chumash). Further subtle differences in the diet of the Neandertal groups from different habitats were detected, with the Neandertals from open-steppe environments having microwear signatures most similar to those of the Fuegians, who relied almost exclusively on meat, and the Neandertals that lived in areas with mixed vegetation having microwear signatures similar to those of the Chumash, whose diet was evidently predominantly meat-based but also included some amounts of plant food. Moreover, although the microwear patterns of the Neandertals that inhabited wooded environments also reflect a predominantly meat-based diet, their diet seems to have been more varied and to have included a slightly higher proportion of plant foods compared to those from more open settings. Overall, these data suggest that plant foods played an important role in the diets of at least some Neandertal groups.

The results of this study show that Neandertals cannot be considered as a single, homogenous sample in terms of their diet. The microwear data indicate that the diets of at least some Neandertals were flexible and that they were able to alter their food choices to cope with the fluctuating climatic conditions throughout their time range, including during MIS 3. The results of this study suggest that the diets of the late surviving Neandertals analyzed here follow the pattern seen for earlier Neandertals in response to climatic, and accompanying paleoecological, changes. Thus, these results do not appear to support a link between the severe climatic fluctuations during MIS 3 alone and the extinction of the Neandertals.

Acknowledgments

We would like to thank the following people for allowing access to Neandertal remains under their care: G. Manzi (Saccopastore 1 and 2, Grotta Breuil 2 and 3, Guattari 2 and 3), I. Pap (Subalyuk 1), C. Schwab and B. Vandermeersch (Saint-Césaire 1, La Quina 20, Marillac), P. Mennecier, V. Laborde, and L. Huet (La Quina 5, La Ferrassie 1), M. Oliva, M. Dočkalová, T. Sojkova, and P. Neruda (Ochoz 1 and Kulna 1), H. de Lumley, M.-A. de Lumley, D. Grimaud-Hervé, A. Viallet, and S. Renault (Petit-Puymoyen 2 and 4, Arcy-sur-Cure II and IVb6 B9, Monsempron 2 and 3), J.-F. Tournepeiche (Rochelot 1098, La Chaise BD8), C. Stringer, R. Kruszynski,

and L. Humphrey (Tabun I), and E. Egocheaga (El Sidrón SDR-005 and SDR-007). We also thank A. Pérez-Pérez for providing casts of the Zafarraya (4) and Vindija (11.39, 11.40a, 11.45, 11.46, 12.1) dental remains and Y. Rak for providing dental molds for Tabun (II), Kebara (2), and Amud (I). Microwear data were collected at the University of Arkansas and we are grateful for R. Scott and K. Krueger for technical assistance. We thank the editor, S. Leigh, the associate editor, and three anonymous reviewers for their helpful comments. This study was supported by the Max Planck Society, the National Science Foundation (0452155 to E. Grine and S. El Zaatari, and 0315157 to P.S. Ungar), and the LSB Leakey Foundation.

Appendix. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.jhevol.2011.05.004.

References

- Ahern, J.M., Karvanić, I., Paunović, M., Janković, I., Smith, F.H., 2004. New discoveries and interpretations of hominid fossils and artifacts from Vindija Cave, Croatia. *J. Hum. Evol.* 46, 27–67.
- Alpers, N., Barzilai, O., Dag, D., Hartman, G., Matskevich, Z., 2000. The age and context of the Tabun I skeleton: a reply to Schwarcz et al. *J. Hum. Evol.* 38, 840–853.
- Antunes, M., 2000. The Pleistocene fauna from Gruta do Figueira Brava: a synthesis. In: Antunes, M. (Ed.), *Last Neanderthals in Portugal: Odontologic and Other Evidence*. Memórias da Academia das Ciências de Lisboa, Lisboa, pp. 259–282.
- Aura Tortosa, J.E., Villaverde Bonilla, V., Pérez Ripoll, M., Martínez Valle, R., Guillem Calatayud, P., 2002. Big game and small prey: Paleolithic and Epipaleolithic economy from Valencia (Spain). *J. Archaeol. Method Th.* 9, 215–268.
- Bœuf, O., 1969. Faune et nouveaux restes humains du gisement moustérien du Petit-Puyrouseau (Charente). *Mém. Soc. Arch. Hist. Charente*, 53–128.
- Bar-Yosef, O., Callander, J., 1999. The woman from Tabun: Garrod's doubts in historical perspective. *J. Hum. Evol.* 37, 879–885.
- Barroso Ruiz, C., Marchi, F., Abdessadok, S., Bailón, S., Desclaux, E., Gregoire, S., Hernandez Carrasquillas, F., Lacomat, F., Lebreton, V., Lecervoisier, B., Moigne, A.-M., Perrenoud, C., Renault-Miskovsky, J., Riquelme Cantal, J.A., Rodriguez Vidal, J., Saos, T., Vernet, J.L., Vilette, P., 2006. Contexte paléocologique, paléoclimatique et paléogéographique des Néandertaliens de la grotte du Boquete de Zafarraya. In: Barroso Ruiz, C., de Lumley, H. (Eds.), *La grotte du Boquete de Zafarraya (Málaga, Andalousie)*. Consejería de Cultura, Junta de Andalucía, pp. 1127–1166.
- Barroso Ruiz, C., Medina Lara, P., Sanchidrian Torti, J.L., Ruiz Bustos, A., Garcia Sanchez, M., 1984. Le gisement Mousterien de la Grotte du Boquete de Zafarraya (Alcaucin, Andalousie). *L'Anthropologie* 88, 133–134.
- Barton, R., 2000. Mousterian hearths and shellfish: late Neanderthal activities in Gibraltar. In: Stringer, C., Barton, R., Finlayson, J. (Eds.), *Neanderthals on the Edge*. Oxbow Books, Oxford, pp. 211–220.
- Beaumont, C., Lacrampe-Cuyabere, F., Maureille, B., Trinkaus, E., 2006. Direct radiocarbon dating and stable isotopes of the Neanderthal femur from Les Rochers de Villeneuve. *Bull. Mém. Soc. Anthropol. Paris* 18, 35–42.
- Belmaker, M., Hovers, E., 2008. A diachronic study of the micromammal remains of Amud Cave, Israel: implications for the paleoecology of a Neanderthal site during MIS 4–3 in the Levant. Abstracts of the 73rd Society for American Archaeology Meeting, 75.
- Binford, L., 1988. Etude taphonomique des restes fauniques de la Grotte Vaufray, couche VIII. In: Rigaud, J.P. (Ed.), *La Grotte Vaufray: Paléoenvironnement, Chronologie, Activités Humaines*. Mém. Soc. Préhist. Fr. vol. 19, pp. 535–546.
- Blackwell, B., Schwarcz, H.P., Debénath, A., 1983. Absolute dating of hominids and Palaeolithic artifacts of the cave of La Chaise-de-Vouthon (Charente). *J. Archaeol. Sci.* 10, 493–513.
- Bocherens, H., Drucker, D., 2003. Reconstructing Neanderthal diet from 120,000 to 30,000 BP using carbon and nitrogen isotopic abundances. In: Patou-Mathis, M., Bocherens, H. (Eds.), *Le rôle de l'environnement dans les comportements des chasseurs-cueilleurs préhistoriques*. BAR Intl. Ser., vol. 1105, pp. 1–7.
- Bocherens, H., Billiou, D., Mariotti, A., Patou-Mathis, M., Otte, M., Bonjean, D., Toussaint, M., 1999. Palaeoenvironmental and palaeodietary implications of isotopic biogeochemistry of late interglacial Neanderthal and mammal bones in Scladina Cave (Belgium). *J. Archaeol. Sci.* 26, 599–607.
- Bocherens, H., Billiou, D., Mariotti, A., Toussaint, M., Patou-Mathis, M., Bonjean, D., Otte, M., 2001. New isotopic evidence for dietary habits of Neanderthals from Belgium. *J. Hum. Evol.* 40, 497–505.
- Bocherens, H., Drucker, D., Billiou, D., Patou-Mathis, M., Vandermeersch, B., 2005. Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: review and use of a multi-source mixing model. *J. Hum. Evol.* 49, 71–87.
- Bocherens, H., Fizet, M., Mariotti, A., Lange-Badre, B., Vandermeersch, B., Borel, J.P., Bellon, G., 1991. Isotopic biogeochemistry (^{13}C , ^{15}N) of fossil vertebrate collagen: application to the study of a past food web including Neanderthal man. *J. Hum. Evol.* 20, 481–492.
- Bouchud, J., 1966. Essai sur le Renne et la climatologie du Paléolithique moyen et supérieur. Imprimerie Magne, Périgueux.
- Boyle, K.V., 2000. Reconstructing Middle Palaeolithic subsistence strategies in the south of France. *Int. J. Osteoarchaeol.* 10, 336–356.
- Bridges, T., 1885. The Yagans of Tierra del Fuego. *J.R. Anthropol. Inst.* 14, 288–289.
- Bruner, E., Manzi, G., 2008. Saccopastore 1: the earliest Neanderthal? A new look at an old cranium. In: Harvati, K., Harrison, T. (Eds.), *Neanderthals Revisited: New Approaches and Perspectives*. Springer, Netherlands, pp. 23–36.
- Callen, E.O., 1969. Les coprolithes de la cabane acheuléenne du Lazaret: analyse et diagnostic. *Mém. Soc. Préhist. Fr.* 7, 123–124.
- Caloi, L., Manzi, G., Palombo, M.R., 1998. Saccopastore, a stage-5-site within the city of Rome. In: *The Eemian – Local Sequences, Global Perspectives Symposium INQUA-SEQS'98*, Kerkrade, The Netherlands, (abstract).
- Cheddadi, R., Rossignol-Strick, M., 1995. Eastern Mediterranean Quaternary paleoclimates from pollen and isotope records of marine cores in the Nile Core area. *Paleoceanogr.* 10, 291–300.
- Conard, N.J., Prindiville, T.J., 2000. Middle Palaeolithic hunting economies in the Rhineland. *Int. J. Osteoarchaeol.* 10, 286–309.
- Conover, W.J., Iman, R.L., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* 35, 124–129.
- Cook, R.J., Farewell, V.T., 1996. Multiplicity considerations in the design and analysis of clinical trials. *J. R. Stat. Soc. Ser. A* 159, 93–110.
- Cordy, J., 1988. Apport de la paléozoologie à la paléocologie et à la chronostratigraphie en Europe du nord-occidental. *L'Homme de Neanderthal. Etudes et Recherches Archéologiques de l'Université de Liège*, Liège, pp. 55–64.
- Daegling, D.V., Grine, F.E., 1999. Terrestrial foraging and dental microwear in *Papio ursinus*. *Primates* 40, 559–572.
- de Jong, D.E., 1988. Climatic variability during the past three million years, as indicated by vegetational evolution in northwest Europe and with emphasis on data from the Netherlands. *Phil. Trans. R. Soc. Lond., B* 318, 603–617.
- de Ponsins, G., 1941. *Kabloon Reynal Reynal & Hitchcock, Inc.*, New York.
- Duport, L., Vandermeersch, B., 1961–1962. Le gisement du Petit-Puymoyen. *Etude archéologique. Mémoires de la Société Archéologique de la Charente*.
- Eisenmann, V., 1992. Systematic and biostratigraphical interpretation of the equids from Qafzeh, Tabun, Skhul and Kebara (Acheuloyabrudian to upper Paleolithic of Israel). *Archaeozoöl.* 1, 43–62.
- El Zaatari, S., 2008. Occlusal molar microwear and the diets of the Ipiutak and Tigara populations (Point Hope) with comparisons to the Aleut and Arikara. *J. Archaeol. Sci.* 35, 2517–2522.
- El Zaatari, S., 2010. Occlusal microwear texture analysis and the diets of historical/prehistoric hunter-gatherers. *Int. J. Osteoarchaeol.* 20, 67–87.
- El Zaatari, S., Grine, F.E., Teaford, M.F., Smith, H.F., 2005. Molar microwear and dietary reconstructions of fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. *J. Hum. Evol.* 49, 180–205.
- Erlanson, J.M., Rick, T.C., Braje, T.J., 2009. Fishing up the food web?: 12,000 years of maritime subsistence and adaptive adjustments on California's Channel Islands. *Pac. Sci.* 63, 711–724.
- Fellag, H., 1996. Etude palynologique de l'abri paléolithique Bourgeois-Delaunay (Chaise, Charente). *Quaternaire* 7, 187–196.
- Finlayson, J., Barton, R., Stringer, C., 2001. The Gibraltar Neanderthals and their extinction. *Trabalhos de Arqueologia* 17. In: Zilhão, J., Aubry, T., Carvalho, A. (Eds.), *Les Premiers Hommes Modernes de la Péninsule Ibérique*. Instituto Português de Arqueologia, Lisbon, pp. 117–122.
- Finlayson, C., Giles Pacheco, F., Rodríguez-Vidal, J., Fa, D.A., Gutierrez López, J.M., Santiago Pérez, A., Finlayson, G., Allué, E., Baena Preysler, J., Cáceres, I., Carrión, J.S., Fernández Jalvo, Y., Gleed-Owen, C.P., Jiménez Espejo, F., López, P., López Sáez, J.A., Riquelme Cantal, J.A., Sánchez Marco, A., Giles Guzman, F., Brown, K., Fuentes, N., Valarino, C.A., Villalpando, A., Stringer, C.B., Martínez Ruiz, F., Sakamoto, T., 2006. Late survival of Neanderthals at the southernmost extreme of Europe. *Nature* 443, 850–853.
- Fizet, M., Mariotti, A., Bocherens, H., Lange-Badre, B., Vandermeersch, B., Borel, J.P., Bellon, G., 1995. Effect of diet, physiology and climate on carbon and nitrogen stable isotopes of collagen in a late Pleistocene anthropic palaeoecosystem: Marillac, Charente, France. *J. Archaeol. Sci.* 22, 67–79.
- Follieri, M., Giardini, M., Magri, D., Sadori, L., 1998. Palynostratigraphy of the last glacial period in the volcanic region of Central Italy. *Quatern. Int.* 47, 317–335.
- Forza, J., de la Rassa, M., Martínez-Maza, C., Sánchez-Moral, S., Cañaveras, J.C., Cuezva, S., Rosas, A., Soler, V., Castro, J., Torres, T., Ortiz, J.E., Juliá, R., Badal, E., Altuna, J., Alonso, J., 2003. La cueva de El Sidrón (Borines, Piloña, Asturias): primeros resultados. *Estud. Geol.* 59, 159–179.
- Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *Am. Mus. Novit.* Nov 3301, 1–36.
- Garrod, D.A., Bate, M.A., 1937. *The Stone Age of Mount Carmel I: Excavations at the Wadi El-Mughara*. Clarendon Press, Oxford.
- Gaudzinski, S., 1998. Large mammal hunting strategies in the Palaeolithic of Europe: a taphonomic approach. In: Bayley, J. (Ed.), *Science in Archaeology: An Agenda for the Future*. English Heritage, London, pp. 47–62.
- Gaudzinski, S., Roebroeks, W., 2000. Adults only. Reindeer hunting at the middle Paleolithic site Salzitter Lebenstedt, northern Germany. *J. Hum. Evol.* 35, 497–521.
- Giddings, J.L., 1967. *Ancient Men of the Arctic*. Secher and Warburg, London.
- Gordon, K., 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. *Am. J. Phys. Anthropol.* 59, 195–215.

- Grün, R., Stringer, C., 1991. Electron spin resonance dating and the evolution of modern humans. *Archaeometry* 33, 153–199.
- Grün, R., Stringer, C., 2000. Tabun revisited: revised ESR chronology and new ESR and U-series analysis of dental material from Tabun C1. *J. Hum. Evol.* 39, 601–612.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15, 783–822.
- Grine, F.E., Ungar, P.S., Teaford, M.F., El Zaatari, S., 2006. Molar microwear in *Præanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. *J. Hum. Evol.* 51, 297–319.
- Gross, H., 1956. Die Umwelt des Neandertalers. In: Tackenberg, K. (Ed.), *Der Neandertaler und seine Umwelt*. Rheinisches Landesmuseum Bonn und Verein von Altertumsfreunden im Rheinlande, Bonn, pp. 68–105.
- Guatelli-Steinberg, D., Larsen, C.S., Hutchinson, D.L., 2004. Prevalence and the duration of linear enamel hypoplasia: a comparative study of Neandertals and Inuit foragers. *J. Hum. Evol.* 47, 65–84.
- Hardy, B.L., 2004. Neanderthal behaviour and stone tool function at the Middle Palaeolithic site of La Quina, France. *Antiquity* 78, 547–565.
- Hardy, B.L., 2010. Climatic variability and plant food distribution in Pleistocene Europe: implications for Neanderthal diet and subsistence. *Quatern. Sci. Rev.* 29, 622–629.
- Henri-Martin, G., 1966. Découverte d'un temporal humain néandertalien dans le gisement de La Quina, Charente. *C.R. Acad. Sci.* 262, 1937–1939.
- Henry, A.G., Brooks, A.S., Piperno, D.R., 2010. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proc. Natl. Acad. Sci.* 108, 486–491.
- Hublin, J.-J., Roebroeks, W., 2009. Ebb and flow or regional extinctions? On the character of Neanderthal occupation of northern environments. *C.R. Palévol* 8, 503–509.
- Hublin, J.-J., Ruiz, C.B., Lara, P.M., Fontugne, M., Reyss, J.-L., 1995. The Mousterian site of Zafarraya (Andalucía, Spain): dating and implications on the Palaeolithic peopling processes of western Europe. *C.R. Acad. Sci., Paris Sér. II* 321, 931–937.
- Huntley, B., Allen, J.R.M., 2003. Glacial environments III: palaeo-vegetation patterns in Last Glacial Europe. In: van Andel, T.H., Davies, W. (Eds.), *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation: Archaeological Results of the Stage 3 Project*. McDonald Institute for Archaeological Research, Cambridge, pp. 79–102.
- Hutchinson, D.L., Larsen, C.S., Choi, I., 1997. Stressed to the max? Physiological perturbation in the Krapina Neandertals. *Curr. Anthropol.* 38, 904–914.
- Jelinek, A.J., Farrand, W.R., Haas, G., Horowitz, A., Goldberg, P., 1973. New excavations at the Tabun cave, Mount Carmel, Israel 1967–1972. *Paléorient* 1, 151–183.
- Kolska Horwitz, L., Hongo, H., 2006. Putting the meat back on old bones: a reassessment of Middle Palaeolithic fauna from Amud Cave (Israel). In: Villa, E., Goulichon, L., Choyke, A.M., Buitenhuis, H. (Eds.), *Archaeozoology of the Near East, VIII. Proceedings of the Eighth International Symposium on the Archaeozoology of Southwestern Asia and Adjacent Areas*, vol. 49, pp. 45–64. *Travaux de la Maison de l'Orient et de la Méditerranée*.
- Kotsakis, T., 1990–1991. Late Pleistocene fossil microvertebrates of Crotta Breuil (Monte Circeo, central Italy). *Quaternaria Nova* 1, 325–332.
- Krueger, K.L., Ungar, P.S., Frayer, D.W., 2010. Teeth as tools? Anterior dental microwear textures of the Krapina Neandertals. *Am. J. Phys. Anthropol.* 50 (Suppl.), 148.
- Lalueza, C., Pérez-Pérez, A., 1993. The diet of the Neanderthal child Gibraltar 2 (Devil's Tower) through the study of the vestibular striation pattern. *J. Hum. Evol.* 24, 29–41.
- Lalueza-Fox, C., Lloreda Sampietro, M., Caramelli, D., Puder, Y., Lari, M., Calafell, F., Martínez-Maza, C., Bastir, M., Fortea, J., de la Rassa, M., Bertranpetit, J., Rosas, A., 2005. Neanderthal evolutionary genetics: mitochondrial DNA data from the Iberian Peninsula. *Mol. Biol. Evol.* 22, 1077–1081.
- Lalueza-Fox, C., Pérez-Pérez, A., Turbon, D., 1996. Dietary inferences through buccal microwear analysis of middle and upper Palaeolithic human fossils. *Am. J. Phys. Anthropol.* 100, 367–387.
- Lavaud-Girard, F., 1993. Macrofauna from the Castelperronian levels at Saint-Césaire, Charente-Maritime. In: Lévêque, F., Backer, A.M., Guilbaud, M. (Eds.), *Context of a Late Neanderthal: Implications of Multidisciplinary Research for the Transition to Upper Paleolithic Adaptations at Saint-Césaire, Charente-Maritime, France*. Prehistory Press, Madison, pp. 71–77.
- Lee, R.B., 1979. *The I Kung San: Men, Women and Work in a Foraging Society*. Cambridge University Press, Cambridge.
- Leroi-Gourhan, A., 1988. Le passage Moustérien-Châtelperronien à Arcy-sur-Cure. *Bull. Soc. Préhist. Fr.* 85, 102–104.
- Leroy, C., Leroi-Gourhan, A., 1993. Pollen analysis at Saint-Césaire. In: Lévêque, F., Backer, A.M., Guilbaud, M. (Eds.), *Context of a Late Neanderthal*. Prehistory Press, Madison, pp. 61–70.
- Lev, E., Kislev, M.E., Bar-Yosef, O., 2005. Mousterian vegetal food in Kebara cave, Mt. Carmel. *J. Archaeol. Sci.* 32, 475–484.
- MacFadden, B.J., Solounias, N., Cerling, T.E., 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. *Science* 283, 824–827.
- Madella, M., Jones, M.K., Goldberg, P., Goren, Y., Hovers, E., 2002. The exploitation of plant resources by Neanderthals in Amud Cave (Israel): the evidence from Phytolith studies. *J. Archaeol. Sci.* 29, 703–719.
- Marean, C., Kim, S.Y., 1998. The Mousterian faunal remains from Kobeh Cave: behavioral implications for Neanderthals and early modern humans. *Curr. Anthropol.* 39 (Suppl.), 79–114.
- Marquet, J.-C., 1988. L'Homme de Néandertal et son environnement dans la moitié ouest de la France d'après les rongeurs. In: Otte, M. (Ed.), *L'Homme de Néandertal. L'Environnement*, vol. 2. ERAUL, Liège, pp. 105–110.
- Marquet, J.-C., 1993. Paléoenvironnement et Chronologie des Sites du Domaine Atlantique Français d'Âge Pléistocène Moyen et Supérieur d'Après l'Étude des Rongeurs. *Les Cahiers de la Claise*, Tours.
- Mellars, P., 2004. Neanderthals and the modern human colonization of Europe. *Nature* 432, 461–465.
- Mercier, N., Valladas, H., 1998. Datations. *Gallia Préhist.* 40, 70–71.
- Mercier, N., Valladas, H., 2003. Reassessment of TL age estimates of burnt flints from the Paleolithic site of Tabun Cave, Israel. *J. Hum. Evol.* 45, 401–409.
- Mercier, N., Valladas, H., Joron, J.L., Reyss, J.-L., Lévêque, F., Vandermeersch, B., 1991. Thermoluminescence dating of the late Neanderthal remains from Saint-Césaire. *Nature* 351, 737–739.
- Miracle, P.T., Lenardić, J.M., Brajković, D., 2010. Last glacial climates, "refugia", and faunal change in Southeastern Europe: mammalian assemblages from Vaternica, Velika pećina, and Vindija caves (Croatia). *Quatern. Int.* 212, 137–148.
- Miskovsky, J.C., Lévêque, F., 1993. The sediments and stratigraphy of Saint-Césaire: contributions to the paleoclimatology of the site. In: Lévêque, F., Backer, A.M., Guilbaud, M. (Eds.), *Context of a Late Neanderthal: Implications of Multidisciplinary Research for the Transition to Upper Paleolithic Adaptations at Saint-Césaire, Charente-Maritime, France*. Prehistory Press, Madison, pp. 7–14.
- Molnar, S., Molnar, I.M., 1985. The incidence of enamel hypoplasia among the Krapina Neandertals. *Am. Anthropol.* 87, 536–549.
- Morin, E., 2004. Late Pleistocene population interaction in western Europe and modern human origins: new insights based on the faunal remains from Saint-Césaire, southwestern France. Ph.D. Dissertation, The University of Michigan.
- Munson, P., Marean, C., 2003. Adults only? A reconstruction of Middle Paleolithic 'prime-dominated' reindeer hunting at Salzgitter Lebenstedt. *J. Hum. Evol.* 44, 263–273.
- Murdock, G.P., 1962. *Ethnographic Atlas*. *Ethnology* 1, 113–134.
- Murdock, G.P., 1963. *Ethnographic Atlas*. *Ethnology* 2, 541–548.
- Murdock, G.P., 1964. *Ethnographic Atlas*. *Ethnology* 3, 199–217.
- Neff, N.A., Marcus, L.F., 1980. *A Survey of Multivariate Methods for Systematics*. American Museum of Natural History, New York (manuscript).
- Ogilvie, M., Curran, B., Trinkaus, E., 1989. Incidence and patterning of dental enamel hypoplasia among the Neandertals. *Am. J. Phys. Anthropol.* 79, 25–41.
- Pérez-Pérez, A., Espurz, A., Bermúdez de Castro, J.M., de Lumley, H., Turbon, D., 2003. Non-occlusal dental microwear variability in a sample of Middle and Late Pleistocene human populations from Europe and the Near East. *J. Hum. Evol.* 44, 497–513.
- Patou-Mathis, M., 1993. Taphonomic and palaeoethnographic study of the fauna associated with the Neanderthal of Saint-Césaire. In: Lévêque, F., Backer, A.M., Guilbaud, M. (Eds.), *Context of a Late Neanderthal*. Prehistory Press, Madison, pp. 79–102.
- Patou-Mathis, M., 2000. Neanderthal subsistence behaviours in Europe. *Int. J. Osteoarchaeol.* 10, 379–395.
- Rabinovich, R., Hovers, E., 2004. Faunal analysis from Amud Cave: preliminary results and interpretations. *Int. J. Osteoarchaeol.* 14, 287–306.
- Recchi, A., 1995. Bird remains from the upper Pleistocene sites of Grotta Breuil (M. Circeo, Latina, Italy) and Riparo Salvini (Terracina, Latina, Italy). *Quaternaria Nova* 5, 81–98.
- Richards, M.P., Schmitz, R.W., 2008. Isotope evidence for the diet of the Neanderthal type specimen. *Antiquity* 82, 553–557.
- Richards, M.P., Trinkaus, E., 2009. Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proc. Natl. Acad. Sci.* 106, 16034–16039.
- Richards, M.P., Pettitt, P.B., Trinkaus, E., Smith, F.H., Paunović, M., Karavanić, I., 2000. Neanderthal diet at Vindija and Neanderthal predation: the evidence from stable isotopes. *Proc. Natl. Acad. Sci.* 97, 7663–7666.
- Richards, M.P., Taylor, G., Steele, T., McPherron, S.P., Soressi, M., Jaubert, J., Orschiedt, J., Mallye, J.B., Rendu, W., Hublin, J.-J., 2008. Isotopic dietary analysis of a Neanderthal and associated fauna from the site of Jonzac (Charente-Maritime), France. *J. Hum. Evol.* 55, 179–185.
- Rink, W.J., Schwarcz, H.P., Lee, H.K., Rees-Jones, J., Rabinovich, R., Hovers, E., 2001. Electron spin resonance (ESR) and Thermal Ionization Mass Spectrometric (TIMS) $^{230}\text{Th}/^{234}\text{U}$ dating of teeth in middle Paleolithic layers at Amud cave, Israel. *Geochim. Geophys. Res. Lett.* 28, 701–717.
- Ryan, A.S., 1993. Anterior dental microwear in late Pleistocene human fossils. *Am. J. Phys. Anthropol.* 16, 171.
- Schwarcz, H.P., Bietti, A., Buhay, W., Stiner, M.C., Grün, R., Segre, A.G., 1991. On the reexamination of Grotta Guattari: Uranium-series and electron-Spin-Resonance dates. *Curr. Anthropol.* 32, 313–316.
- Schwarcz, H.P., Buhay, W., Grün, R., 1990–1991. Absolute dating of sites in coastal Lazio. *Quaternaria Nova* 1, 51–67.
- Schwarcz, H.P., Simpson, J.J., Stringer, C., 1998. Neanderthal skeleton from Tabun: U-series data by gamma-ray spectrometry. *J. Hum. Evol.* 35, 635–645.
- Schwartz, J.H., Tattersall, I., 2002. *The Human Fossil Record: Terminology and Craniodental Morphology of Genus Homo (Europe)*. Wiley-Liss, New York.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. *J. Hum. Evol.* 51, 339–349.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436, 693–695.

- Sealy, J.C., 2006. Diet, mobility, and settlement pattern among Holocene hunter-gatherers in Southernmost Africa. *Curr. Anthropol.* 47, 569–595.
- Segre, A.G., 1983. Geologia quaternaria e Paleolitico nella bassa valle dell'Aniene, Roma in L'Uomo di Saccopastore e il suo ambiente. I Neandertaliani nel Lazio. *Riv. Antropol.* 62, 87–98.
- Semal, P., Rougier, H., Crevecoeur, I., Jungels, C., Flas, D., Hauzeur, A., Maureille, B., Germonpré, M., Bocherens, H., Pirson, S., Cammaert, L., de Clerck, N., Hambucken, A., Higham, T., Toussaint, M., Van der Plicht, J., 2009. New data on the late Neandertals: direct dating of the Belgian Spy fossils. *Am. J. Phys. Anthropol.* 138, 421–428.
- Sergi, S., Ascenzi, A., 1955. La mandibola neandertaliana Circeo III. (mandibola B). *Riv. Antropol.* 42, 337–403.
- Silberbauer, G.B., 1981. *Hunter and Habitat in the Central Kalahari Desert*. Cambridge University Press, Cambridge.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*. W.H. Freeman and Company, New York.
- Speth, J.D., Tchernov, E., 1998. The role of hunting and scavenging in Neandertal procurement strategies: new evidence from Kebara Cave (Israel). In: Akazawa, T., Aoki, K., Bar-Yosef, O. (Eds.), *Neandertals and Modern Humans in Western Asia*. Plenum Press, New York, pp. 223–239.
- Speth, J.D., Tchernov, E., 2001. Neandertal hunting and meat-processing in the Near East: evidence from Kebara cave (Israel). In: Stanford, C.B., Bunn, H.T. (Eds.), *Meat-Eating and Human Evolution*. Oxford University Press, Oxford, pp. 52–72.
- Speth, J.D., Tchernov, E., 2002. Middle Paleolithic tortoise use at Kebara cave (Israel). *J. Archaeol. Sci.* 29, 471–483.
- Stiner, M.C., 1994. *Honor Among Thieves*. Princeton University Press, Princeton.
- Teaford, M.F., 1986. Dental microwear and diet in two species of *Colobus*. In: Else, J., Lee, P. (Eds.), *Proceedings of the Tenth Annual International Primatological Conference. Primate Ecology and Conservation*, vol. 2. Cambridge University Press, Cambridge, pp. 63–66.
- Teaford, M.F., O'Leary, M., 1992. Dental microwear and diet of mesonychids. *J. Vert. Paleontol.* 12, 45A.
- Teaford, M.F., Oyen, O.J., 1989a. Differences in rate of molar wear between monkeys raised on different diets. *J. Dent. Res.* 68, 1513–1518.
- Teaford, M.F., Oyen, O.J., 1989b. In vivo and in vitro turnover in dental microwear. *Am. J. Phys. Anthropol.* 80, 447–460.
- Teaford, M.F., Oyen, O.J., 1989c. Live primates and dental replication: new problems and new techniques. *Am. J. Phys. Anthropol.* 80, 73–81.
- Teaford, M.F., Robinson, J.G., 1989. Seasonal or ecological zone differences in diet and molar microwear in *Cebus nigrivittatus*. *Am. J. Phys. Anthropol.* 80, 391–401.
- Timbrook, J., 1993. Island Chumash ethnobotany. In: Glassow, M.A. (Ed.), *Archaeology on the Northern Channel Islands of California: Studies of Subsistence, Economics and Social Organization*. Coyote Press, Salinas, pp. 47–62.
- Tournepiche, J.-F., Couture, C., 1999. The hyena den of Rochelot cave (Charente, France). *Monographien des Römisch-Germanischen Zentralmuseums* 42, 89–101.
- Tzedakis, P.C., Bennett, K., 1995. Interglacial vegetation succession: a view from southern Europe. *Quatern. Sci. Rev.* 14, 967–982.
- Ungar, P.S., 1996. Dental microwear of European Miocene catarrhines: evidence for diets and tooth use. *J. Hum. Evol.* 31, 355–366.
- Ungar, P.S., Brown, C.A., Bergstrom, T.S., Walker, A., 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. *Scanning* 25, 185–193.
- Ungar, P.S., Grine, F.E., Teaford, M.F., 2008. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE* 3, e2044.
- Ungar, P.S., Grine, F.E., Teaford, M.F., El Zaatari, S., 2006. Dental microwear and diets of African early *Homo*. *J. Hum. Evol.* 50, 78–95.
- Ungar, P.S., Merceron, G., Scott, R.S., 2007. Dental microwear texture analysis of Varswater bovids and early Pliocene paleoenvironments of Langebaanweg, western Cape Province, south Africa. *J. Mamm. Evol.* 14, 163–181.
- Ungar, P.S., Scott, R.S., Grine, F.E., Teaford, M.F., 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. *Phil. Trans. R. Soc. Lond., B* 365, 3345–3354.
- Valladas, H., Joron, J.L., Valladas, G., Arensburg, B., Bar-Yosef, O., Belfer-Cohen, A., Goldberg, P., Laville, H., Meignen, L., Rak, Y., Tchernov, E., Tillier, A.-M., Vandermeersch, B., 1987. Thermoluminescence dates for the Neanderthal burial site at Kebara in Israel. *Nature* 330, 159–160.
- Valladas, H., Mercier, N., Hovers, E., Froget, L., Joron, J.L., Kimbel, W.H., Rak, Y., 1999. TL dates for the Neanderthal site of the Amud cave, Israel. *J. Archaeol. Sci.* 26, 259–268.
- Vallois, H.V., 1952. Les restes humains du gisement Moustérien de Monsempron. *Ann. Paléorient* 38, 100–120.
- van Andel, T., 2002. The climate and landscape of the middle part of the Weichselian Glaciation in Europe: the Stage 3 project. *Quatern. Res.* 57, 2–8.
- van Andel, T., Tzedakis, P.C., 1996. Paleolithic landscapes of Europe and environs 150,000–25,000 years ago: an overview. *Quatern. Sci. Rev.* 15, 481–500.
- Walker, P.L., 1996. Integrative approaches to the study of ancient health: an example from the Santa Barbara channel area of Southern California. In: Pérez-Pérez, A. (Ed.), *Notes on Population Significance of Paleopathological Conditions: Health, Illness and Death in the Past*. Fundació Uriach, Barcelona, pp. 97–105.
- Walker, P.L., Teaford, M.F., Ungar, P.S., 1994. Enamel microwear differences between species of *Proconsul* from the early Miocene of Kenya. *Am. J. Phys. Anthropol.* 18 (Suppl.), 202–203.
- Wild, E.-M., Paunovic, M., Rabeder, G., Steffan, I., Steier, P., 2001. Age determination of fossil bones from the Vindija Neanderthal site in Croatia. *Radiocarbon* 43, 1021–1028.
- Wolpoff, M.H., Smith, F.H., Males, M., Radović, J., Rukavina, D., 1981. Upper Pleistocene human remains from Vindija cave, Croatia, Yugoslavia. *Am. J. Phys. Anthropol.* 54, 499–545.