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Ecogeographic Variation in Neandertal Dietary Habits:

Evidence from Microwear Texture Analysis

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Abstract of the Dissertation

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For over 100,000 years, Neandertals inhabited a variety of ecological zones across western Eurasia, between glacial and interglacial conditions. To elucidate the still poorly understood effects of climatic change and variability, and possible competition on the Neandertal subsistence patterns, this study employed dental microwear texture analysis to reconstruct the dietary habits of 54 Neandertal, Pre-Neandertal, and early Upper Paleolithic (EUP) modern human specimens from 28 sites in western Eurasia. Microwear signatures of seven modern hunter-gatherer groups (n = 155) of known and diverse diets were analyzed for comparative purposes.

Microwear signatures of Neandertals and Pre-Neandertals are correlated with variation in vegetation-cover, such that individuals from cold-steppe/tundra vegetation had less complex microwear surfaces than those from forested environments. The microwear pattern of the EUP fossils did not differ significantly from those of the Pre-

Neandertal groups and northern and central European Neandertals, which suggests that the former had a more varied diet. However, significant differences in microwear signatures were found between the southern European Neandertals and the EUP fossils. In accord with the stable isotope results, microwear analysis classifies Neandertals as top-level carnivores. However, dental microwear analysis detected some subtle dietary differences. Thus, the microwear signatures of Neandertals and Pre-Neandertals from steppe/tundra vegetation are similar to meat-eating Fuegians from comparable habitats, whereas those of Neandertals and pre-Neandertals from forested environments resemble the Chumash, who inhabited a Mediterranean-like environment. Neandertals from the deciduous forests of southern Europe have a microwear signature that falls within the ranges of Australian and African aborigines with mixed diets. EUP fossils have microwear signatures that resemble those of both the modern Chumash and Fuegians.

This dissertation is dedicated to my parents,

Mona and Rachid

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Chapter 1

Introduction

Temporal and geographical spread of the Neandertals

Neandertals were very successful throughout western Eurasia for more than a hundred thousand years before they suddenly disappeared around 28 kyr (Zilhão 2001). Over this period of time, the Neandertals had to cope with sometimes harsh and severely changing environments over oxygen isotope stages (OIS) 6 through 3 (van Andel and Tzedakis 1996). Nevertheless, at the beginning of OIS 2, they were effectively replaced by more modern human populations. Documenting the dietary habits of the Neandertals through time and across the various glacial and interglacial periods is the key to understanding their capabilities to adapt and survive for such a lengthy period. It has been argued that modern humans were behaviorally superior to the Neandertals and out-competed them for resources. A study of the Neandertal dietary variability over time is essential to determine whether there was any evidence of dietary shifts that could be related to competition at the time of the advent of modern humans in Eurasia.

Brief introduction to the climatic changes during the Ice Ages in Europe

Neandertals lived during the alternating glacial/interglacial cycles of the Middle and Late Pleistocene. A clear picture of the climate and environment of western Eurasia

during this period has been provided by the oceanic sediment records (Shackleton 1967; Shackleton 1969; Shackleton 1975; Shackleton 1977; Shackleton 1987), the land based ice cores records (1992; Johensen et al. 1972; 1993; Jouzel et al. 1987; 1989), and long pollen sequences from a number of European and Middle Eastern sites (Behre and van der Plicht 1992; Cheddadi and Rossignol-Strick 1995; de Beaulieu and Reille 1984; 1992a; 1992b; Follieri et al. 1998; Guiot et al. 1989; Mangerud et al. 1981; Pérez-Obiol and Juliá 1994; Pons and Reille 1988; Reille and de Beaulieu 1990; Rossignol-Strick and Planchais 1989; Tzedakis 1993; Tzedakis 1994; Tzedakis and Bennett 1995; van Zeist and Bottema 1991; Watts 1985; Wijmstra 1969; Woillard 1978a; Woillard and Mook 1982). Climatic reconstructions show that during any single OIS, western Eurasia was divisible into several climatic zones and that the climate of any one area varied between glacial and interglacial times. The fossil and archaeological records indicate that the Neandertals were able to survive in most of these western Eurasian Ice Age environments. Their remains are associated with warm forested environments as well as more cold and open ones. Changes in vegetation cover in response to climatic changes must have certainly affected food availability. During glacial times, plant and animal species in the areas mostly affected by the cold (i.e., northern Europe) became extinct. This is not the case in the warmer southern/Mediterranean part of the continent, which is characterized by continuity in the plant and animal records (Tzedakis and Bennett 1995). During interglacial periods, there was colonization by new species and re-colonization from refugia by older community members of plants and animals from the south. These colonization and re-colonization events resulted in the mixing of elements from steppe and forest, creating strange associations of animals in northern Europe and giving each

interglacial period an individual character different from the ones before it (de Jong 1988). All interglacials, however, followed a broadly similar succession for forest regeneration. The Neandertals would have had to adapt to these changes to be able to survive. However, the role that these changes played in their diets is still unclear. Food availability strongly affects the social structure of a group, as well as population density, settlement patterns, and the territory that a group occupies. Thus, the effects of the changes in the environment on the Neandertal life might be addressed by examining dietary variation among Neandertal groups from different ecological zones.

Brief introduction to the previous studies on Neandertal diets

The dietary habits of the Neandertals are still poorly understood. Reconstructions have been attempted through the analysis of associated Middle Paleolithic faunal assemblages (Auguste 1992; Binford 1988; Chase 1986; Chase 1989; Gaudzinski 1995; Gaudzinski 1998; Gaudzinski and Roebroeks 2000; Hoffecker et al. 1991; Jaubert et al. 1990; Marean and Kim 1998; Mellars 1996; Munson and Marean 2003; Stiner 1994) and plant remains (Hardy 2004; Lev et al. 2005; Madella et al. 2002). However, the faunal assemblages studied have concentrated on the mode of exploitation (hunting versus scavenging) of the Neandertals. Very few studies have looked at plant exploitation during the Middle Paleolithic. Also, proving the dietary use of these plants has been shown to be very difficult if not almost impossible. Dietary reconstructions also have been attempted by analogy through the study of cranial morphology (Brace 1964; Coon 1962; Demes 1987; Franciscus and Trinkaus 1995; Howells 1975; Martin 1923; Puech

1979; Rak 1986; Siffre 1923; Spencer and Demes 1993; Trinkaus 1983; Trinkaus 1987; Trinkaus 1992; Ungar et al. 1997; Wallace 1975), but linking morphological factors directly to dietary adaptations is fraught with difficulty. Studies of dental enamel hypoplasia have also been used to infer the amount of nutritional stress that some Neandertal groups faced (Cunha et al. 2004; Guatelli-Steinberg et al. 2004; Hutchinson et al. 1997; Molnar and Molnar 1985; Oglivie et al. 1989; Skinner 1996). All of these studies have treated the Neandertals as a single group, failing to consider any possible dietary differences resulting from different ecogeographic conditions. Stable isotopes in Neandertal bones have also been examined (Balter and Simon in press; 1999; 2001; Bocherens and Drucker 2003; Bocherens et al. 2005; Bocherens et al. 1991; Fizet et al. 1995; Richards et al. 2000; Schoeninger 1982), but these analyses were based on samples from a limited number of sites. Finally, buccal microwear of various Neandertal teeth has been analyzed in an attempt to better understand their dietary habits (Lalueza-Fox and Pérez-Pérez 1993; Lalueza-Fox et al. 1993; Lalueza-Fox et al. 1996; Pérez-Pérez et al. 2003). However, the usefulness of this technique in dietary reconstructions is still uncertain.

Brief description of the potential of dental microwear analysis

Numerous studies have demonstrated the potential of occlusal dental microwear to yield direct evidence of tooth use and diet in both extant as well as extinct species (Daegling and Grine 1999; El Zaatari et al. 2005; Grine 1986; 1987; Grine and Kay 1988; Grine et al. 2006; Ryan 1981; Ryan and Johanson 1989; Scott et al. 2006; Scott et al.

2005; Taylor and Hannam 1987; Teaford 1985; 1986; 1993; Teaford and Glander 1991; Teaford and Robinson 1989; Teaford and Walker 1984; Ungar 1994; 1996; Ungar et al. 2006; Walker 1976; Walker et al. 1994). Although variations in microwear patterns can be attributed to various factors [e.g., the characteristics of the abrasives ingested with food (Daegling and Grine 1999; Teaford and Glander 1991), enamel microstructure (Maas 1991), and properties of jaw biomechanics (Gordon 1982)], the mechanical properties of the diet itself have been considered to be the primary cause of these patterns. Studies have shown that specific diets and ingestive behaviors leave characteristic patterns of microscopic scratches and pits on extant primate teeth. Occlusal microwear analysis has been shown to be a useful tool for detecting slight differences in diets of closely related species (e.g., Teaford 1986; 1993). Thus, occlusal microwear has the capability to differentiate short-term variations in diet (Teaford and Oyen 1989a). The established methods of occlusal dental microwear analysis have now been enhanced by the analysis of three-dimensional surface thus increasing accuracy, objectivity and repeatability of the measurements (Scott et al. 2006; Scott et al. 2005; Ungar et al. 2003). This new technique for the examination of microwear, dental microwear texture analysis, uses confocal microscopy coupled with scale-sensitive fractal analysis for the study of surface complexity.

The study of dental microwear is of particular relevance to the Neandertals because it has the ability to detect seasonal (and other ecological) differences in the diet of a single species (Teaford and Glander 1991; 1996; Teaford and Robinson 1989). Despite the potential of dental microwear for elucidating ecological dietary differences among primate and hominid species, this technique has not yet been applied to the

Neandertals and their contemporaries from Pleistocene sites in Europe and the Middle East.

Aims of the study

This study entails the reconstruction of Neandertal dietary habits from different sites in Europe and the Middle East using the occlusal microwear of their permanent molar teeth. The occlusal microwear of other fossil humans, namely those that both preceded and followed the Neandertals in Europe, and pene-contemporaneous anatomically modern *Homo sapiens* in the Levant, was also analyzed. Modern human populations with known dietary habits provided a comparative and interpretive database for this study.

This project has four aims. The first is to better understand the effects (if any) of climatic changes on Neandertal diets. As will be discussed in Chapter 2, the climatic reconstructions suggest that western Eurasian environments differed greatly between glacial and interglacial times, and that during the same oxygen isotope stage various parts of western Eurasia had different ecological conditions. Possible variations in Neandertal diets in response to climatic changes were tested by comparing the microwear signatures of Neandertal groups from glacial periods to those from interglacial ones from a single geographical area. In addition, microwear patterns were compared among Neandertal groups dating to the same time period but from different geographical zones.

The second aim is to compare Neandertal microwear signatures to those of the other fossil hominins analyzed, namely those that a) predated the Neandertals in Europe,

b) were contemporary with them in the Levant, and c) postdated them in Europe. Like the Neandertals, the pre-Neandertal groups from Europe also experienced harsh and fluctuating environments. Remains of these groups, although not as widespread as those of the Neandertals, have been discovered from both glacial and interglacial periods from different areas. Comparisons of microwear signatures of Neandertals and Pre-Neandertal groups will help determine whether they experienced similar dietary excursions in response to environmental fluctuations.

Comparisons between the microwear patterns of the Mousterian anatomically modern humans from the Levant and the different Neandertal groups should help to determine whether their dietary habits differed. For this purpose, the microwear data from the Skhul specimens were compared to those for Neandertals from the Levant and Europe that experienced similar environmental conditions.

The early Upper Paleolithic specimens analyzed in this study were recovered from sites in central and southern Europe dated to the end of OIS 3 and the beginning of OIS 2. Therefore, they broadly overlapped with the last surviving Neandertal groups from St. Césaire, Zafarraya, and Vindija. The microwear signatures of the anatomically modern humans from the Levant were also compared to those of the early Upper Paleolithic modern humans. Comparisons of the microwear patterns of Neandertals, anatomically modern Levantine humans and early Upper Paleolithic humans may lead to a better picture of possible differeces in their dietary habits.

The third aim is to document the microwear signatures of modern human groups with known but diverse dietary habits. The microwear signatures of archaeological and historic hunter-gatherer groups from different geographical locations and different

environmental conditions were compared. Good ethnographic or historic data relating to dietary habits of the selected modern groups are available.

The forth aim is to infer the dietary proclivities of the Neandertals and the other fossil human groups. This was attained by comparing the occlusal microwear signatures of the fossils to those of the modern human populations. The carbon/nitrogen isotope signatures suggest that Neandertals, or at least those from OIS 3, were largely carnivorous. The occlusal microwear data may reveal whether these Neandertals were more similar to modern carnivorous hunter-gatherers than to those with other dietary habits.

Finally, this study speaks of the degree of competition between Neandertals and modern humans as a possible cause of Neandertal disappearance. A better understanding of the pattern of Neandertal diet across the various glacial and interglacial periods will help establish whether there was a noticeable shift in their diets that occurred with the advent of modern humans in Europe. A competitively induced shift might be inferred if the microwear signatures of the last surviving Neandertals differ significantly from those of the early Upper Paleolithic fossils and from earlier Neandertals under similar ecogeographic conditions.

Chapter 2

World of the Neandertals: Climate and Vegetation

Reconstruction of Pleistocene environments

The pattern of glacial/interglacial fluctuations is accompanied by changes in temperature, wind force and direction, precipitation, animal life and vegetation, and in sea level and coastline exposure. All these factors must have played a major role in the life of the Neandertals. Therefore, to better understand the behavior of the Neandertals, it is important to have a detailed understanding of the world they inhabited.

The following reconstructions of the Pleistocene climate and environments of western Eurasia are based on the analyses of the oxygen isotope record from deep-sea sediments (Shackleton 1967; Shackleton 1969; Shackleton 1975; Shackleton 1977; Shackleton 1987) and from ice cores drilled out of the glaciers in Greenland (1992; Johensen et al. 1972) and Antarctica (1993; Jouzel et al. 1987; 1989). The oxygen isotope record is supplemented by pollen analysis from terrestrial and marine (deep-sea and lake) sediments. The most important sites that have yielded long pollen sequences are shown in Figure 1. For comparative purposes, the vegetation cover that would have existed today in Europe and the Levant in the absence of agriculture in shown in Figure 2a.

The oxygen isotope stages: an explanation

Climatic change that is inferred from the deep-sea sediments is based on the changing chemical composition (in particular variation of the content of oxygen-16 and oxygen-18) of the shells of species of foraminifera and other sea dwelling microorganisms. The record of the oxygen isotope ratios ($^{18}O/^{16}O$) reflects world ice volume (Duplessy 1978; Shackleton 1967). During their short lifetime, the foraminifera extract oxygen from the seawater and incorporate it into their shells. After their death they fall to the ocean floor, keeping a record of the seawater's variation in ^{16}O and ^{18}O over time. Since ^{18}O is heavier than ^{16}O, water molecules containing ^{16}O evaporate faster than those containing ^{18}O. In colder climates (i.e., glacial times), ^{16}O becomes locked in the ice sheets leaving the seawater enriched in ^{18}O. Thus, the shells of microorganisms from glacial periods show a higher ratio of ^{18}O compared to ^{16}O. During warmer or interglacial times, the ice melts and the previously trapped ^{16}O is released into the oceans, thus raising the level of ^{16}O relative to ^{18}O in the seawater and in the shells of the microorganisms. Therefore, the changing ratios of ^{18}O and ^{16}O in the shells of the foraminifera reflect the climatic fluctuations between cold and warm periods (Shackleton 1967; Shackleton 1975; Shackleton 1987).

Figure 3 shows the Oxygen Isotope Stage (OIS) curve of Core V19-30 (Bassinot et al. 1994; Shackleton and Opdyke 1973). The odd numbers refer to warm or interglacial stages while the even numbers refer to cold or glacial stages. What follows here is a detailed description of the conditions during oxygen isotope stages (OIS) 7-3 dating to the period between 242 and 24 kyr.

Conditions during oxygen isotope stages 7-3

OIS 7 (242-186 kyr)

Examined specimens

      Pontnewydd 1 and 12, and Steinheim 1 pre-Neandertals.

Ice spread, sea levels and climate

      Oxygen isotope stage 7 is divided into 3 parts: a, b, and c. Sub-stage 7b started around 230 kyr and lasted for 10-15 kyr. It is identified as a short ice age between two periods of the strongest maxima at 250-240 kyr and 220-215 kyr (Ninkovich and Shackleton 1975; Ruddiman and Mcintyre 1982). Pacific and Atlantic ice cores document that OIS 7b witnessed a major increase in on-land ice volume, which accumulated relatively fast (in 10 kyr) and lasted for a very short period of time (10-15 kyr) (Ninkovich and Shackleton 1975; Ruddiman and Mcintyre 1982). Compared to other interglacials, this one witnessed low sea levels overall.

Flora

      Turner (1975) reconstructed the vegetation in Europe during this time as follows. In continental Europe, alder and pine were abundant at the beginning of this interglacial. Oak, elm, and basswood were less prominent than during any other interglacial. During the later phase mixed-oak species dominated. Fir expanded in Europe and was more

widespread and abundant in this interglacial than in the Holocene or in OIS 5e, reaching

Denmark and Britain. At Hoxne in Britain, an episode rich in non-tree pollen occurs

during the middle part of the interglacial, pointing to a period during which open ground

was prevelant.

OIS 6 (186-127 kyr)

Examined specimens

Tabun II and possibly Tabun I Neandertals.

Ice spread, sea levels and climate

At this stage the Northern ice sheets were among the most extensive of the whole

Pleistocene. They had a much longer duration compared to those of OIS 2, and the ice

margin extended, on average, around 2º to 3º south of OIS 2 ice limits (van Andel and

Tzedakis 1996). Sea levels were slightly lower than those of OIS 2, and were 100-140m

below present levels (van Andel and Tzedakis 1996). The Vostok record shows that the

overall temperature during OIS 6 was around 6ºC lower than the Holocene (Jouzel et al.

1993). This is supported by temperature reconstructions provided by long pollen

sequences from French sites such as La Grande Pile and Les Echets. These two sites had

an average annual temperature between 1-2ºC during OIS 6 whereas today they have an

average annual temperature of around 9.5ºC (Guiot et al. 1989). Precipitation at these

two sites was also lower than that today. During OIS 6, La Grande pile had 300mm of

annual precipitation and Les Echets had 200mm, whereas the annual precipitation at these two sites today is 1080mm and 830mm respectively (Guiot et al. 1989).

<u>Flora</u>

At the beginning of OIS 6, the tree cover in Europe fluctuated. The development of more extreme climatic conditions in the later part of this stage led to a mainly treeless landscape in the continent. As illustrated in Figure 2b, a polar desert occupied the area south of the ice margin, while the rest of Europe had a discontinuous herbaceous plant cover (van Andel and Tzedakis 1996). The corridor between the Alpine and Scandinavian ice caps had a mixture of tundra and steppe elements dominated by grasses, chenopods, and sedges for which no modern analogue exists (van Andel and Tzedakis 1996; van Andel 1996). An extensive, arid and cold steppe environment existed in southern and Mediterranean Europe, which has pollen records comprising mostly *Artemisia[1]*, chenopods, and grasses. White sage and weed plants were present at the time in Greece (pollen from Tenaghi Philippon), indicating that environments were cold and arid (Smit and Wijmstra 1970). Scattered temperate tree populations survived in sheltered areas such as the mountains of Italy and the western Balkans where temperature variations were not extreme and precipitation was sufficient for these trees to survive (Bennett et al. 1991; Tzedakis 1993). Woodland populations were also present in some southern areas, such as the Iberian Peninsula. The tree cover in southern and Mediterranean Europe consisted of coniferous populations mainly in the northern Balkans, northern Italy and some in northeast Spain. Deciduous trees were present further south, with evergreens in

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[1] This genus of plants include between 200-400 species of herbs and shrubs which grow in the temperate climates of dry or semi-dry habitats.

the extreme south and coastal lowlands (van Andel and Tzedakis 1996). The Levant was covered by semi-desert vegetation. The Taurus Mountains, however, may have provided refugia for warmth-loving trees (Cheddadi and Rossignol-Strick 1995).

OIS 5 (127-71 kyr)

This stage is divided into 5 parts: 5e, 5d, 5c, 5b and 5a with the last one being the most recent.

OIS 5e (130-115 kyr)

The Last interglacial, OIS 5e is known as the Eemian in Northern Europe, Ipswichian in Britain, Riss-Würm in France, and Mikulino in Russia.

Examined specimens

Saccopastore 1 and 2 Neandertals.

Ice spread, sea levels and climate

Overall, OIS 5e was warmer than the Holocene (van Andel and Tzedakis 1996), when glacials retreated to their present positions or even further back. Sub-polar and boreal bioclimatic zones were displaced by several hundreds to a few thousands of kilometers north of their present limits (LIGA 1991). Sea-levels were close to those of today (Chappell and Shackleton 1986; LIGA 1991; Martinson et al. 1987), with the

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exception of the Eemian Sea which was very much higher than the present North and

Baltic seas (Mangerud et al. 1979; Mangerud et al. 1981; Miller and Mangerud 1986;

Nilsson 1983). Between 126 and 116 kyr, when the Eemian Sea was at its highest level

(around 30 m higher than present), it occupied the entire Baltic basin and connected the

North Sea with the White Sea and the Arctic Ocean, thus isolating Scandinavia

(Forsstrom et al. 1988; Mangerud et al. 1979) and providing a long and highly productive

northern coastline (van Andel and Tzedakis 1996). For the Eemian Sea to have been

created, the rate of sea level rise would have been around 20m/kyr, which is twice that of

the present postglacial rise (Zagwijin 1983). This supports a rapid deglaciation at the end

of OIS 6 and beginning of OIS 5e. Baumann et al. (1995) state that the Scandinavian Ice

Sheet decayed within 2000 years or less at this transitional period.

Climatic conditions were similar to those of today but with average annual

temperatures some 2 or 3ºC higher (Dansgaard et al. 1993; Jouzel et al. 1987; LIGA

1991; Lorius et al. 1985; Sejrup and Larsen 1991; Shackleton 1987). The $\delta^{18}O$ values

from Crete (Thunell and Williams 1983) and the western Mediterranean (Cornu et al.

1993) show a temperature increase of 3ºC starting at 127 kyr. During the first 5000 years

of this stage, temperatures rose by at least 10-15ºC (Larsen et al. 1995; Zagwijin 1983).

However, temperatures dropped in the second half of OIS 5e and this was reflected in

vegetation changes (Guiot et al. 1989). Sea surface temperatures show that sub-tropical

waters almost reached the British Isles (Sutcliffe 1985).

Flora

This interglacial started with the re-colonization of trees from refugial centers (van Andel and Tzedakis 1996). Pollen records from over 100 separate locations in different parts of Europe (Bowen 1978; de Beaulieu and Reille 1984; LIGA 1991; Müller et al. 2003; Sánchez Goñi et al. 2005; Watts 1988; West 1977; Woillard 1978b; Zagwijin 1990) show a similar pattern of forest development with a few minor variations. van Andel and Tzedakis (1996) describe the vegetation of the European continent during this interglacial as being a succession that began with deciduous oak and elm species. These species were followed first by hazel, and then yew which became prominent north of the Alps. After that the horebeam forest spread across all of the European continent. The Horebeam expansion was soon accompanied by the expansion of fir, then spruce and pine indicating the return to cooler conditions at the end of the interglacial. Towards the end of OIS 5e, a brief double peak of fir or spruce interrupted by pine peaks have been recorded at some sites (e.g., Devès Plateau, Les Echets, La Grande Pile) (Tzedakis 1994). The oak/elm interval in southern Europe was followed by a major expansion of Mediterranean forest characterized by wild olive and evergreen oak. The olive in the circum-Mediterranean region reached values higher than those of the Holocene (van Andel and Tzedakis 1996). Open and relatively treeless conditions were widespread only at the beginning and end of the interglacial.

Fauna

The animal migration during this stage was very rapid. Arctic fauna was enriched by megafauna, such as woolly mammoth and rhinoceros, which existed at the northern part of Europe (Stringer and Gamble 1993). Semi-tropical species like hippopotamus and

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European pond tortoise appear in the faunal records from northern Europe as well (Bowen 1978; LIGA 1991; Stuart 1982; West 1977; Zagwijin 1990).

OIS 5d-5a (115-71 kyr)

The Early Glacial, started after the warm period of OIS 5e, when the climate deteriorated slowly between OIS 5d and 5a (van Andel and Tzedakis 1996). The decrease in temperature was accompanied by a decrease in megafauna in northern Europe, which became increasingly inhabited by grazing species such as red deer and horse (Stringer and Gamble 1993). The vegetation cover became more open, but remained relatively wooded during this time. In the middle latitudes, however, there were severe disruptions in tree cover (Stringer and Gamble 1993).

Examined specimens

Skhul 7 anatomically modern human.

OIS 5d and OIS 5b

Oxygen isotope stage 5d is known as Herning or Melisey I whereas OIS 5b is known as Rederstall or Melisey II.

Ice spread, sea levels and climate

For both stadials, the ice cover was of very short duration and it was not as widespread as the ice cover of glacial periods. The ice volume during these two stadials only reached about half that of the Last Glacial Maximum (Shackleton 1977; Shackleton 1987). The Scandinavian ice-sheet was not extensive (Mangerud 1991a; Mangerud 1991b; Mangerud et al. 1981) and, judging from the lack of ice-rafted deposits in the Norwegian Sea[2], Baumann et al. (1995) argued that the ice front did not reach the coast of Norway. OIS 5d witnessed the continuation of the drop in sea-level which started at the end of OIS 5e; during OIS 5b the sea levels dropped again.

OIS 5d and 5b were cold and dry (Guiot et al. 1989). The mid summer temperatures of northern Europe (from the Netherlands through northern Germany to central Poland) hardly rose over 8ºC which is 8-10ºC less than the present temperature of the area (Klotz et al. 2004; Zagwijin 1990). The south had less temperature reduction with an average depression year round of 5-6ºC (Guiot et al. 1989). This shows that, unlike the preceding interglacial period, there was a sharp pattern of climatic gradients from northern to southern Europe (Sejrup and Larsen 1991).

Flora

Vegetation from pollen records show that the areas in northern and western Europe had essentially open vegetation with patches of birch-pine forest and an increasing component of woodland further to the south and east across the continent (Klotz et al. 2004; Zagwijin 1990). Tundra vegetation dominated in northwest

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[2] High ice rafted material in the cores imply that many icebergs from the Scandinavian ice sheet were drifting in the Norwegian Sea because the ice sheet was large and/or was breaking up. Therefore, fluctuations ice rafted deposits fluctuations are proposed to reflect oscillations of the ice sheet. The highest numbers of icebergs in the Norwegian sea are reported at 150-124 kyr, 58-50 kyr, and 28-10 kyr (Baumann et al. 1995).

Scandinavia. The area from southern Denmark to the Rhone valley was dominated by grasses, sedges or other tundra-like plants. Areas further to the south and east the areas were dominated by high frequencies of more steppe species such as *Artemisia,* meadow-rue*,* chenopods[3] (Behre 1989; Zagwijin 1990). The eastern Mediterranean region had cold dry chenopods and *Artemisia* Steppe conditions (Cheddadi and Rossignol-Strick 1995). Conditions during OIS 5b were more severe than those of OIS 5d. This is confirmed by the pollen records from southern Europe, which show a greater expansion of chenopods and *Artemisia,* suggesting an increase in aridity (Follieri et al. 1998). However, evidence from all areas document the existence of localized patches of more hardy trees such as pine, birch and willow. This implies that the climatic conditions never became quite as severe as those during OIS 4 and 2.

OIS 5c and OIS 5a

Oxygen isotope stage 5c is known as the Brorup or St. Germain I and OIS 5a is known as Odderade or St. Germain II. These two periods are interstadials.

Ice spread, sea levels and climate

The volume of the major ice masses during these periods was reduced to approximately half that attained during the colder episodes of 5d and 5b. During OIS 5c, part of the Scandinavian ice-sheet may have melted (Mangerud 1991b). The ice volume during both interstadials, however, was still greater than during fully interglacial periods

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[3] Any plant of the goosefoot family of flowering plants which includes around 1400 species including spinach, sugar beet, and chard

(Shackleton 1977; Shackleton 1987). OIS 5a witnessed a gradual global increase in ice volume beyond that of OIS 5c. The sea levels rose again during both interstadials with OIS 5c having higher sea levels than OIS 5a (Bard et al. 1990; Picket et al. 1985; Smart and Richards 1992).

Both interstadials (5c and 5a) saw a sharp increase in world wide temperatures (Shackleton 1977; Shackleton 1987). July temperatures ranged from 12ºC (6º below those of the present) in southern Scandinavia and northern Germany to 18-20ºC (1-2ºC below those of the present) in the southern parts of France and along the Atlantic coast (Klotz et al. 2004; Zagwijin 1990). This pattern is confirmed by the multivariate analyses of the climate and the vegetation patterns proposed by Guiot et al. (1989; 1993) for pollen sequences at La Grande Pile and Les Echet. The pollen records also show that during OIS 5c and 5a there were some climatic fluctuations (with cold episodes lasting 1000-2000 years). Tree cover was reduced, giving way to essentially open vegetation (Behre 1989; de Beaulieu and Reille 1984; Woillard 1978b; Zagwijin 1990). Zagwijn (1990) indicates that during these short episodes, climatic conditions might have fallen into levels similar to those prevailing during OIS 5d and 5b.

Flora

The interstadials OIS 5c and 5a are very clear in the Grande Pile Pollen profile from the Voges Mountains in France (Guiot et al. 1989; Woillard 1978b; Woillard and Mook 1982) and in the Lake Ioannina core 249 from northwestern Greece (Tzedakis 1993). In northern pollen diagrams they appear as a two phase - birch followed by pine - succession. The pollen sequences from various European sites show that these two

interstadials had very similar vegetation cover. Pollen records from sites in southern

Europe such as La Grande Pile (Woillard 1978b; Woillard and Mook 1982), Ioannina 249

(Tzedakis 1993) and Monticchio (Watts et al. 1996) show that tree expansion was

relatively rapid in these regions of Europe implying that their refugia were relatively

close.

Northern Europe (Netherlands, Britain, Denmark, Northern Germany), which was

previously occupied by open or shrub tundra communities, witnessed a migration of

conifer forests with species of pine, spruce, fir, larch and birch. South central Europe and

France had an expansion of a mixed forest with warm-loving deciduous trees (Behre

1989; Emontspohl 1995; Müller et al. 2003). A deciduous forest with Mediterranean

elements existed south of the Alps (Follieri et al. 1998; Pons and Reille 1988; Tzedakis

1994; Wijmstra 1969). Southwest Europe (Rhone valley and western Alps) had more

warmth-demanding deciduous species until pine and spruce reasserted themselves with

the next cold phase (de Beaulieu and Reille 1984; Woillard 1978b). As for the eastern

Mediterranean region, it was occupied by Mediterranean mixed evergreen and deciduous

woodland, but landscapes were more open than those of OIS 5e (Cheddadi and

Rossignol-Strick 1995).

OIS 4 (71-57 kyr)

This period is known as the Pleniglacial.

Examined specimens

Guattari 3, Subalyuk 1 and Kebara 2 Neandertals.

Ice spread, sea levels and climate

The climatic deterioration which started at the end of OIS 5e culminated in a large

global increase of ice volume at the beginning of the OIS 4 (van Andel and Tzedakis

1996). Although there is evidence that the continental ice sheets expanded during this

stage far beyond the limits reached during the earlier cold periods of 5d and 5b (Chappell

and Shackleton 1986; Shackleton 1977; Shackleton 1987), their exact limits remain

uncertain because their margins are obscured by later erosion and/or burial by the ice

sheets of OIS 2 (Butzer 1971; Chappell and Shackleton 1986; Shackleton 1987). The

issue of the spread of the ice sheets during this period is still highly controversial. A

reconstruction by Andersen and Manderud (1989) presents two possible limits for the ice

during OIS 4 (Figure 2). It is still unclear if there was an advance of the Alpine ice caps

corresponding to that of Fennoscandia ice-sheet (de Beaulieu et al. 1991; Frenzel 1991).

Glacial deposits from OIS 4 might have also existed in Denmark (Strand-Petersen and

Kronborg 1991), Poland (Mojski 1991), Estonia (Liivrand 1991) and northwest Germany.

In Scotland, a small ice-cap or glacier deposit exists underneath OIS 3 interstadial beds

(Sutherland and Gordon 1993). England, however, was probably ice-free until 25 kyr

ago (Ehlers et al. 1991).

Climatic reconstructions based on pollen analyses from France indicate that

annual temperatures were 12-13˚C lower and precipitation was 650-800 mm less than at

the present (Guiot et al. 1989). Sea surface temperature in the north Atlantic fell to at

least 3-4˚ lower than those attained during any of the preceding glacials (Imbrie and

Imbrie 1979; Sancetta et al. 1973). Pollen records from La Grande Pile and Les Echets show that during OIS 4, dry and continental climates prevailed in the area (de Beaulieu and Reille 1984; Woillard 1978b; Woillard and Mook 1982). Northern areas such as Holland, Denmark and north Germany had average temperatures well below freezing for much of the year, and mid summer temperatures around 5°C (Behre 1989; Zagwijin 1990).

Flora

This period was probably similar to sub-stages 5b and 5d, but it represented a more extreme version in terms of vegetation changes, and especially the diminution of trees in the Mediterranean area (Watts et al. 1996). As illustrated in Figure 2d, the vegetation records show that the response to the expansion of the Scandinavian ice sheet was complex (van Andel and Tzedakis 1996). At the OIS 5a/4 boundary there was a brief time of open vegetation which was followed by the Ognon warm phase characterized by renewed expansion of conifers in France and southern Germany (Woillard 1978b). South of the Alps, juniper also increased. The lower temperatures which resulted from the expansion of the Fennoscandian ice-sheet led to the appearance of extensive open vegetation at the end of OIS 4 (van Andel and Tzedakis 1996). Central Europe became completely treeless (Müller et al. 2003). Pollen records from La Grande Pile and Les Echets show that conditions during OIS 4 were steppic (Artemisia and Chenopods) (de Beaulieu and Reille 1984; Woillard 1978b; Woillard and Mook 1982). In southern Europe, the tundra and cold arid steppe tree populations expanded into areas previously occupied by warmth-loving tree populations (Tzedakis 1993). The eastern

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Mediterranean region had a similar sequence of events where there was a slight

expansion of evergreen oak and other Mediterranean elements at the beginning of OIS 4,

and then the landscape became covered by a semi-desert vegetation (Cheddadi and

Rossignol-Strick 1995). Areas such as Holland, Denmark and northern Germany became

treeless, open/tundra (even polar deserts in some places) during the coldest phases of OIS

4 (Behre 1989; Zagwijin 1990). Because pollen production in northern Europe at that

time was low due to the types of vegetation and arctic style peat formation, no pollen

records are available for that area (Zagwijin 1992).

OIS 3 (57-24 kyr)

This stage is known as the Interpleniglacial.

Examined specimens

The Neandertals of Amud 1, La Quina 5 and 20, Sidrón 1 and 2, Spy 1, Breuil 2,

St. Césaire 1, Zafarraya, Vindija 11.39, 11.45, 11.46, 11.409, and 12.1, and Ochoz 1 and

the early Upper Paleolithic individuals of Mladeč 1, 2, 4, 8, Stetten 1, Combe Capelle 1,

Předmostí, Pavlov 3, Dolni Věstonice 13, 14, 16, 31, and Barma Grande 1, 2 and 5.

Ice spread, sea levels and climate

Evidence of an increase in ice-rafted sediments in the Norwegian Sea implies a

retreat of the Fennoscandia ice-sheet at the beginning of OIS 3 (Baumann et al. 1995).

This ice sheet remained limited to only a part of Fennoscandia until OIS 2. Just like the

limits of the ice sheets during OIS 4, those of OIS 3 are controversial (Andersen and Manderud 1989; Donner 1995; Mangerud 1991b). There is evidence, however, that the ice volume decreased somewhat at the beginning of OIS 3 but that it increased gradually over the next 30 kyr. Similarly, sea levels fluctuated at the beginning of this period and then, towards the end of OIS 3, they gradually fell (Bard et al. 1990).

The climate of this interglacial was predominantly mild but not as mild as that of OIS 5 (Martinson et al. 1987; Shackleton 1977; Shackleton 1987). It is difficult to reconstruct the environment of this period due to the sharp oscillations of climatic events (van Andel 2002). These brief oscillations appear clearly in the Greenland ice core sequences and in the sea surface temperatures recorded from the North Atlantic deep-sea cores (Bond et al. 1993). In fact, the best records of these oscillations can be seen in the recent high-resolution studies of two long ice cores (GRIP and GISP2) from central Greenland (Boulton 1993; Dansgaard et al. 1993; GRIP-members 1993; Kerr 1993). The oxygen isotope record shows that OIS 3 can be divided into around 30 climatic phases (Dansgaard et al. 1993). These warm and cold phases were mostly short-lived lasting between 500-2000 years each (Dansgaard et al. 1993). There were approximately 12 significant warm periods, where temperatures rose by 5 to 8º C in less than 50 years or so (Dansgaard et al. 1993; Grootes et al. 1993). The pollen record from La Grande Pile suggests that, mean annual temperatures for the warm period at 36-39 kyr were about 4˚C less than that of today, and that precipitation was 200-400 mm less than today (Guiot et al. 1989). Some periods were more prolonged (2000-4000 years) and had even higher temperatures.

<u>Flora</u>

The cold/dry phases were dominated by desert-steppe or grassland vegetation (depending on the location in Europe), whereas the warm/humid periods were dominated by coniferous and deciduous forests in central and southern Europe and steppe-tundra vegetation in the northern parts of Europe (Alfano et al. 2003). Evidence from the deep sea cores around the Iberian Peninsula indicate that temperate tree populations and shrubs were always present in the area during OIS 3 (d'Errico and Sánchez Goñi 2003; Roucoux et al. 2005). The continuous presence of trees in local areas led to their rapid expansion during the warmer parts of this interglacial (d'Errico and Sánchez Goñi 2003; Roucoux et al. 2005). The shorter phases of OIS 3 can be detected in pollen records from southern Europe, but they are not represented in the records from northern and central Europe north of the Alps because these phases were too brief for trees to migrate into these areas (Guiot et al. 1989; Müller et al. 2003). The longer periods, however, are represented in the pollen records from many areas. They can also be seen in high resolution records of sea surface temperatures (Behre 1989; Behre and van der Plicht 1992; Bond et al. 1993; de Beaulieu and Reille 1984; Guiot et al. 1989; Labeyrie 1984; Paterne et al. 1984; Sancetta et al. 1973; Woillard 1978b; Zagwijin 1990).

Conditions for the relatively warm period between 36-39 kyr can be considered as being representative of most of the mild phases of OIS 3 (Figure 2e). These periods make up around half of this stage (van Andel and Tzedakis 1996). Pollen records show that in northern Germany, the Netherlands and eastern Baltic there was a shrub tundra vegetation with species like birch, willow and juniper (Behre 1989), and scattered spruce near St. Petersburg (Liivrand 1991). Eastern France and the Alpine foreland were

covered by open pine, spruce and birch woodland. North of the Alps, deciduous trees

seem to have been present (de Beaulieu and Reille 1984; de Beaulieu and Reille 1992a;

de Beaulieu and Reille 1992b; Grüger 1989; Reille and de Beaulieu 1990; van Andel and

Tzedakis 1996).

　　With regards to Mediterranean Europe, Catalonia was occupied by pine woodland

with some deciduous oak (Pérez-Obiol and Juliá 1994), southern Spain was occupied by

evergreen and deciduous oak populations along with pine and juniper (Pons and Reille

1988), central and southern Italy and northern Greece were covered by deciduous

woodland with species like oak, hazel, beech, basswood, and elm (Follieri et al. 1998;

Rossignol-Strick and Planchais 1989; Watts 1985), and southern Greece was dominated

by the expansion of deciduous and evergreen oak and pine and juniper populations. "The

OIS 3 Mediterranean woodland was open in character; however, highest tree densities are

recorded in only a few places where moisture was sufficient and soil conditions optimal

such as in northwestern Greece and central Italy" (van Andel and Tzedakis 1996).

Finally, the Eastern Mediterranean region was dominated by evergreen woodland

expanded within a mainly semi-desert landscape (Cheddadi and Rossignol-Strick 1995;

van Zeist and Bottema 1991).

Chaper 3

Previous Studies of Neandertal Diets

Archaeological evidence

Faunal remains

Most of the information on Neandertal subsistence has been provided through the analyses of faunal assemblages from Middle Paleolithic sites (Auguste 1992; Binford 1988; Chase 1986; 1989; Gaudzinski 1995; 1998; Gaudzinski and Roebroeks 2000; Hoffecker et al. 1991; Jaubert et al. 1990; Marean and Kim 1998; Mellars 1996; Munson and Marean 2003; Stiner 1991; 1994). However, most of these studies have approached the faunal assemblages with the aim of understanding their mode of exploitation (hunting verses scavenging). Since both hunting and scavenging imply that the Neandertals were getting meat, the arguments in relation to the modes of exploitation in Middle Paleolithic sites will not be discussed here. Rather, by dividing the European continent into three main zones, the northern, central and southen/Mediterranean regions, this chapter will concentrate on the species most likely consumed by the Neandertals.

The resources in the Neandertal world differed by both geographic and temporal zones. The climatic changes during the Pleistocene affected the distribution of animal species just as they affected plant communities. During extreme cold episodes, some of the animal species disappeared, while others became more widespread (Table 1). The

cold episodes had a greater effect on the northern part of the European continent than the southern and Mediterranean regions, where there was a more continuous pattern of animal occupation. Since conducting a site-by-site analysis of the faunal remains is beyond the scope of this dissertation, I present the results of studies summarizing Neandertal subsistence patterns from faunal assemblages from much of the Middle Paleolithic of northern and central Europe (Patou-Mathis 2000), southern France (Boyle 2000) and central Spanish Mediterranean regions (Aura Tortosa et al. 2002).

Patou-Mathis (2000) summarizes the results of faunal assemblages from 323 northern and central European sites. This study shows that the Neandertals from these areas focused their hunting on large to medium sized herbivores. Specialized hunting appears to have been quite frequent especially in western Europe and in the northern part of Central Europe as early as OIS 7 (Patou-Mathis 2000). Faunal assemblages from the majority of the levels are dominated by a single species, or by a cohort of two or three species, and horse appears to have been the Neandertal's preferred game (Patou-Mathis 2000). To a lesser extent, other species, such as mammoth, red deer, bison, ibex, Merck's rhinoceros (especially during OIS 5e), and reindeer, were also the focus of hunts (Patou-Mathis 2000). All these species are large, gregarious and migratory and, except for Merck's rhinoceros, are typical of cold climates and steppic or grassland (open) environments (Patou-Mathis 2000). Medium-sized forest dwelling herbivores are better represented in the faunal assemblages only during OIS 5e (Patou-Mathis 2000). Small species and species uncommon in the local environment were sometimes preferred, but small game hunting remained very rare (Patou-Mathis 2000).

Boyle (2000) summarizes the evidence from faunal assemblages from sites in southern France dating between 130-30 kyr. Assemblages from this area suggest that the Neandertals were primarily hunting large quantities of medium-sized herbivores, such as red deer, ibex, roe deer, wild boar, tahr and chamois, along with larger species such as bison, horse, rhino, and elephant (Boyle 2000). This evidence indicates that the Neandertals from the region of southern France exploited both woodland and open environment animals.

Middle Paleolithic faunal assemblages from the majority of Spanish Mediterranean sites dating to between OIS 5 and OIS 3 are characterized by high diversity of species (including deer, horse and to a lesser degree antelope) hunted by Neandertals (Aura Tortosa et al. 2002). In this region, Neandertals selectively hunted large and medium-sized herbivores; evidence of small game hunting is minimal (Aura Tortosa et al. 2002).

Studies of faunal remains yield indirect evidence of meat consumption by Neandertals, but they are insufficient to provide a full comprehension of their diets since they do not speak to its floral aspect. In addition, the interpretation of the faunal remains from the Middle Paleolithic sites is highly debated (Gaudzinski and Roebroeks 2000; Munson and Marean 2003). Another problem is that the archaeological record is not always perfect. Sometimes the animal bones may have disappeared entirely from the archaeological site (the case of the majority of Paleolithic open air sites) or they might have been subjected to varying degrees of selective taphonomic destruction that can distort their survival in complex and significant ways. For these reasons, researchers have

explored alternative or complimentary methods to better understand the dietary habits of hominins in general, and Neandertals in particular.

Plant remains

Finding evidence of plant use from archaeological contexts is difficult, and proving that these plants were collected for food is an almost impossible task since plants were almost certainly exploited for various purposes (e.g., fuel, bedding, etc.). Floral remains are rarely preserved, and when they do survive it is usually on the microscopic, rather than the macroscopic scale. Evidence of plant remains from the Paleolithic of western Eurasia has been found in sediments and on stone tools (Hardy 2004; Hardy and Kay 1998; Hardy et al. 2001; Lev et al. 2005; Madella et al. 2002; Manson et al. 1994). When found on stone tools, these remains can give information on the exploitation of plants as well as the use of the tools (Hardy 2004). In sediments, plant remains can be in the form of carbonized, mineralized or waterlogged remains (Madella et al. 2002).

The dietary use of plants has been inferred from very few sites dating to the Middle Palaeolithic in western Eurasia. In their study of charred seeds and other vegetal remains from the Kebara cave in the Middle East, Lev et al. (2005) argue that the Neandertals collected a variety of plants for dietary purposes. These included legumes and wild grasses, fruits and seeds. These authors also suggest that the inhabitants of Kebara collected legumes in the Spring and acorns and pistachio nuts in the Fall (Lev et al. 2005). In a study of the phytoliths from Amud cave, Madella et al. (2002) argue for the possibility that the Neandertals selectively collected mature grass panicles for the

consumption of their seeds. These limited studies, although they attempt to highlight the importance of a usually overlooked part of the Neandertals diet, cannot provide sufficient information on the dietary proclivities of these hominins.

Cranial and dental morphology

Neandertal dental and facial morphology exhibits unique characteristics, some of which have been used in an attempt to elucidate their dietary habits. Thus, midfacial prognathism and the shoveled and heavily worn anterior teeth suggest an extensive use of the anterior dentition (Brace 1964; Coon 1962; Demes 1987; Howells 1975; Puech 1979; Rak 1986; Siffre 1923; Trinkaus 1983; 1987; 1992; Ungar et al. 1997; Wallace 1975) or paramasticatory use of the these teeth (Demes 1987; Howells 1975; Rak 1986; Ryan 1993; Smith 1983; Smith and Paquette 1989; Spencer and Demes 1993; Trinkaus 1983; 1987; 1992). Some researchers argue that other Neandertal adaptations represent masticatory specialization to process hard abrasives in the diet (Puech 1979; Siffre 1923; Wallace 1975).

The retromolar gap, which is common among Neandertals, has been linked to high loading on the anterior teeth. Spencer and Demes (1993) linked the retromolar space to changes in the dental arcade resulting from the anterior migration of the molars and the muscles of mastication (masseter and temporalis), and thus the relative posterior positioning of the anterior teeth.

Incisor beveling has also been noted in many Neandertal specimens since the earliest discoveries of the species. This beveling in the maxillary teeth is combined with

heavy wear, large teeth dimensions, massive lingual tubercles and pronounced shoveling (Ungar et al. 1997). There have been arguments that these features might be a result of very high levels of abrasives in the Neandertals diet (Martin 1923; Puech 1979; Siffre 1923; Wallace 1975), or a result of a high rate of their use as a "third hand" for holding, processing and manipulating objects (Brace 1962; 1964; Coon 1962). In an analysis of the formation of this incisor wear, Ungar et al. (1997) related this to three different factors: differences in initial incisor procumbency, where the Neandertals may have had more procumbent maxillary incisors at a given stage of wear than modern populations, labial separation of the maxillary and mandibular incisal occlusal surfaces during edge-to-edge bite in Neandertals, and/or the degree of rotation of the maxillary incisors (or the degree of "posterior tipping") which itself is a result a greater degree of interproximal wear. The interproximal wear provides some space within the dental arcade for the incisors to rotate lingually.

Several authors have claimed that Neandertal dentitions are characterized by having thinner than expected enamel (Molnar et al. 1993; Ramirez Rozzi 1993; Smith 1991; Zilberman et al. 1992; Zilberman and Smith 1992a; 1992b). Some workers link this observation to the possibility that the Neandertals suffered from suboptimal health with mineral metabolic disorders that affected the enamel formation (Molnar et al. 1993), while others argue that it is a result of an accelerated crown formation rate (Ramirez Rozzi 1993; Ramirez Rozzi 1996; Ramirez Rozzi and Bermúdez de Castro 2004). All these studies employ lateral radiographs for measuring enamel thickness. However, it has been shown that this method does not provide accurate measurements (Grine et al. 2001). Using a different methodology (micro-computed and micro-focal computed tomography),

recent studies demonstrate that Neandertals and modern humans do not differ in their enamel thickness (Macchiarelli et al. 2006; Olejniczak and Grine 2005).

Dental pathology

Dental enamel hypoplasia, which appears to be seen with high frequency among Neandertals, is a defect in enamel that results in less quantity of enamel than normal. Although this defect is linked to general or specific nutritional imbalances, it may also be caused by genetic anomalies or environmental forces such as trauma, parturition stresses and infectious diseases (Oglivie et al. 1989). Therefore, hypoplasia, which may be manifest on the teeth as serial pits or a linear groove in the tooth, may provide information on the level of biological stress on the sample and the approximate age distribution of that stress (Oglivie et al. 1989). The frequency and possible cause of dental enamel hypoplasia among Neandertals has been considered in six studies (Cunha et al. 2004; Guatelli-Steinberg et al. 2004; Hutchinson et al. 1997; Molnar and Molnar 1985; Oglivie et al. 1989; Skinner 1996).

Molnar and Molnar (1985) studied enamel hypoplasia in a sample from Krapina, and found that a high percentage of these teeth thus affected, suggesting that this population faced a high degree of stress which they argue is dietary. Ogilvie et al. (1989) examined a sample of 669 teeth of European and Near-Eastern Neandertals, although 40% of these teeth came from the site of Krapina. The results also suggested that Neandertals have a high incidence of dental enamel hypoplasia (36% by tooth and 75% by individual), which is comparable to the most severely stressed recent human

agricultural sample, the Mississipian agricultural population of North America. In Neandertals, the frequency of affected deciduous teeth and first permanent molars is low, implying that they faced a high level of stress that began at weaning and continued through adolescence. Oglivie et al. (1989) opine that such a pattern is probably linked to a very high nutritional stress as a result of inefficient foraging strategy among Middle Paleolithic peoples.

Hutchinson et al. (1997) also examined the teeth from Krapina. Although they found the percentages of affected individuals and teeth to be similar to those reported by Molnar and Molnar (1985) and Ogilvie et al. (1989), Hutchinson et al. (1997) suggest that the degree of stress the Krapina Neandertals faced was not as extreme as postulated by Molnar and Molnar (1985) and Ogilvie et al. (1989). Hutchinson et al. (1997) found that the Krapina enamel defect frequencies fell close to those of a recent North American archaeological sample that experienced seasonally based resource shortages. The frequency of defects on the Neandertal teeth, in fact, was lower than that of the North American Atlantic coast sample, which faced extreme nutritional stress.

In a recent study, Guatelli-Steinberg et al. (2004) examined 18 Neandertals from Krapina and southern France for linear enamel hypoplasia and found that 7 of the 18 individuals (38.9%) were affected by this defect. This incidence is similar to an Inuit sample from Point Hope, Alaska, which suggests that the Neandertals were no more stressed than modern foragers (Guatelli-Steinberg et al. 2004). An analysis of enamel hypoplasia of the Atapuerca – Sima de los Huesos site showed that 4.6% of the teeth were affected (Cunha et al. 2004). This low percentage implies that this sample experienced a low level of developmental stress (Cunha et al. 2004).

The aforementioned studies included more permanent than deciduous teeth; however, Skinner (1996) compared the frequency of dental hypoplasia in immature individuals from two periods: one from the Middle Paleolithic (N=59 individuals consisting of 128 deciduous and 154 permanent teeth), and the second from the Upper Paleolithic (N=47 individuals consisting of 162 deciduous and 125 permanent teeth). The Middle Paleolithic sample consisted primarily of Neandertal fossils from Europe, but it also included specimens from Qafzeh and Irhoud. He found that the Upper Paleolithic sample was more variable in the types and timing of the enamel defects. The Middle Paleolithic sample showed a peak of enamel hypoplasia defect at 3.5 years of age, whereas the most common occurrences in the Upper Paleolithic were at 0.5 years of age.

The available enamel hypoplasia data have been interpreted to mean that at least some Neandertal populations experienced considerable nutritional stress. However, the cause of this stress is still unclear; it is possible that it was related to nutritional factors.

Stable isotope analyses

An Explanation

Stable isotope analyses have been widely employed in archaeological research as a direct method to infer diets. Stable isotopes of carbon and nitrogen are mostly used in paleodietary reconstructions. There are two stable isotopes each of carbon (^{12}C, ^{13}C) and nitrogen (^{14}N, ^{15}N), with ^{12}C and ^{14}N being by far the most common in nature. Small differences in the ratios of these isotopes (referred to as δ^{13}C and the δ^{15}N values) can be

measured in bone collagen samples smaller than 1 milligram (Lajtha and Marshall 1994).

Since bone collagen is disproportionately produced from the protein portion of the diet,

its stable isotope analysis permits quantitative estimates of several dietary components.

In adults, bone collagen is constantly being resorbed and replenished, taking about ten

years for all the collagen in long bones to be replaced. Thus, the isotopic composition of

adult human bone collagen reflects dietary averages over at least the last several years of

an individual's life (Ambrose 1993; Schwarcz and Schoeninger 1991).

Carbon isotopic signatures can be used to identify the types of plants at the base

of the food web, and are dependent on the kind of environment where plant

photosynthesis occurs (Richards and Hedges 1999; Schoeninger et al. 1983). For

terrestrial environments, the different types of photosynthetic pathways (Calvin-Benson

cycle for C_3 plants and Hatch-Slack cycle for C_4 plants) result in different $\delta^{13}C$ values for

plants. C_3 plants fix carbon from ribulose diphosphate into three-carbon acids, utilizing

the enzyme ribulose-diphosphate carboxylase while C_4 plants fix CO_2 into

phosphoenolpyruvate using the enzyme phosphoenolpyruvate carboxylase to yield four

carbon acids. C_3 plants include trees, shrubs, and grasses from temperate regions, and

will have $\delta^{13}C$ values of some -26.5‰ (Lajtha and Marshall 1994). In some forested

areas, however, a canopy effect occurs due to incomplete atmospheric mixing, and this

results in even more negative carbon isotope ratios (van der Merwe and Medina 1991).

Typically, grasses native to hot, arid environments follow the C_4 (Hatch-Slack)

photosynthetic pathway, and have $\delta^{13}C$ values of about -12.5‰ (Lajtha and Marshall

1994). The $\delta^{13}C$ values in the collagen of herbivores are influenced by the kinds of

plants they eat, and the $\delta^{13}C$ values of carnivores and omnivores are influenced by the

isotopic composition of the animals they pray on. In addition to differentiating diets

based on C_3 and C_4 plants, carbon isotopic ratios can be used to identify relative amounts

of marine verses terrestrial protein in the diet (Chisholm et al. 1982). Marine organisms

are more enriched in ^{13}C than terrestrial ones (Chisholm et al. 1982), and this enrichment

will be reflected in the $\delta^{13}C$ values of humans or animals that feed on marine species.

The nitrogen isotopic value, $\delta^{15}N$, is a measure of the amount of plant compared

to animal food in the diet. The nitrogen isotope ratios for plants depend primarily on how

they obtain their nitrogen - by symbiotic bacterial fixation or directly from soil nitrates -

and these values are similarly passed along through the food chain accompanied by an

approximately 2-4‰ positive shift for each trophic level (Ambrose and DeNiro 1986;

DeNiro and Epstein 1981; Schoeninger and DeNiro 1984). The increase in $\delta^{15}N$ values

from one trophic level to the next is more pronounced in marine ecosystems which have

long food chains (Keegan and DeNiro 1988; Schoeninger and DeNiro 1984). Thus,

human consumers of terrestrial plants and animals typically have bone collagen $\delta^{15}N$

values around 6-10‰, whereas consumers of fish (e.g., seals and sea lions) may have

$\delta^{15}N$ values of 15-20‰ (Katzenberg and Weber 1999; Schoeninger et al. 1983).

Nitrogen isotope ratios of plants vary according to altitude, rainfall, and other factors

(Ambrose 1991; Heaton et al. 1986; Sealy et al. 1987). This variation will also affect

primary consumers and consumers higher up in the food chain. Indeed, herbivores from

arid regions of Africa have higher $\delta^{15}N$ values than closely related herbivores from areas

with more rainfall. Therefore, since $\delta^{15}N$ values fluctuate through time and space

(Iacumin et al. 1996), it is critical to establish a site-specific isotopic baseline to interpret

hominin data. Such a baseline is usually provided by analyzing the faunal remains

associated with the human skeletal remains. Establishing an isotopic baseline is particularly important in coastal areas where marine and riverine resources, and/or C_4 plants, may have been available for direct or indirect consumption by humans.

Neandertal diet from stable isotopes

Studies of stable isotopes provide some direct information on Neandertal diets (1999; 2001; Bocherens and Drucker 2003; 2005; Bocherens et al. 1991; Fizet et al. 1995; Richards et al. 2000; Schoeninger 1982). Stable isotope analyses have been recovered from the bones of only ten adult and two immature Neandertal specimens to date (Table 2) from six sites (Les Pradelles, previously known as Marillac, and Saint Césaire in France, Scladina Cave, Awirs Cave and Spy Cave in Belgium, and Vindija in Croatia) (Bocherens et al. 1999; 2001; Bocherens and Drucker 2003; 2005; 1991; Fizet et al. 1995; Richards et al. 2000). All of these fossils, with the exception of those from Scladina Cave, are dated to OIS 3. The Scladina Neandertal child comes from layer 4A, dated to the Eemian interglacial (OIS 5e) by absolute dating and to the Saint-Germain II interstadial (OIS 5c) by palynological correlations (Bocherens et al. 1999). The second Neandertal examined from Scladina Cave has been relocated from layer 1B (OIS 3) as described by Bocherens et al. (2001) to layer 3 (OIS 5b) (Bocherens et al. 2005). The carbon-nitrogen stable isotope data for all the Neandertals and most of the associated fauna are presented in Figure 4.

It should also be noted that although the reconstruction of diet of twelve Neandertal specimens has been attempted using stable isotope analysis, the signatures of

only five of these specimens can be considered reliable for this purpose (Bocherens et al. 2005). Thus, for the first Neandertal specimen examined from Les Pradelles (Bocherens et al. 1991), its amino acid composition was determined instead of its carbon and nitrogen percent because such determinations on collagen were not routinely performed at that time. The isotopic signature of this specimen might therefore be slightly shifted as a result of chemical degradation (Bocherens et al. 2005). The signature of another specimen, M100, from Les Pradelles also might not be reliable because its carbon and nitrogen concentrations are lower than those of fresh collagen (Bocherens et al. 2005). The problem with the reliability of the interpretation of the isotopic signatures of the Vindija Neandertals rests on the lack of isotopic data from contemporary faunal material from the same site or from other sites close by. Because comparing the isotopic values of hominins with those of animals from a different age and/or geographical location can be misleading, the presence of isotopic data from coeval fauna are essential (Bocherens et al. 2005). The interpretation of the isotopic signature of the Neandertal from Scladina Cave layer 1B cannot be considered reliable due to its relocation to layer 3 which is much older than layer 1B. Comparisons of the isotopic values of the fauna from layers 1A and 1B might not produce accurate conclusions of paleodietary reconstructions especially that the environments of these layers 1 and 3 might have been different (Bocherens et al. 2005). To date, no stable isotope data for faunal remains from layer 3 are available (Bocherens et al. 2005). Finally, weaning might have affected the isotopic signature from the Engis child, resulting in its very high $\delta^{15}N$ value (Bocherens et al. 2001; 2005). At this age (5-6 years) the effect of weaning would still be reflected in the isotopic signature of an individual resulting in high $\delta^{15}N$ value since milk is one trophic level higher than a post

40

weaning diet (Bocherens et al. 2001). Therefore, isotopic data from only five

Neandertals, three from Les Pradelles, one from Saint Césaire and one from Spy are

considered reliable for dietary reconstructions. Although there are no faunal remains

associated with the Spy Neandertal fossil, isotopic signatures from the Scladina layer 1A

faunal remains can be used instead because these faunal remains are contemporary with

the Spy fossil (Bocherens et al. 2005).

Nevertheless, the results of the carbon-nitrogen analyses are consistent. All twelve

Neandertal specimens that have been examined are identified as top level carnivores

(1999; 2001; Bocherens and Drucker 2003; 2005; Bocherens et al. 1991; Fizet et al.

1995; Richards et al. 2000), even though the fossils are geographically and

chronologically dispersed and the data from some of them might not be very reliable.

The Neandertals have δ^{15}N values (between 8.4 and 12.6) that are closer to those of

carnivorous than herbivorous animals (Figure 4). Sea or fresh water fish will increase the

δ^{15}N values of their consumers, but the Neandertal δ^{15}N values are not as high as would

be expected if they included such foods (1999; 2001; Bocherens and Drucker 2003; 2005;

Bocherens et al. 1991; Fizet et al. 1995; Richards et al. 2000). The Neandertal δ^{13}C

values suggest that they were probably preying on more open-ranging herbivores (1999;

2001; Bocherens and Drucker 2003; 2005; Bocherens et al. 1991; Fizet et al. 1995;

Richards et al. 2000). The stable isotope studies have tried to highlight the variations in

signatures among the specimens from Les Pradelles (Bocherens et al. 1991; Fizet et al.

1995), between the Engis child and other Neandertals (Bocherens et al. 2001) and

between the two Scladina specimens (Bocherens et al. 1999; 2001), but such variation is

not excessive, falling within the ranges exhibited by some groups of associated fauna. It

is perhaps noteworthy that the carbon/nitrogen signatures of the Scladina 4A Neandertal, which comes from the forested environment of OIS 5 in the Wallonia region of Belgium, is very similar to those of Neandertals from the more open environments of OIS 3 (Figure 4).

Stable isotopes other than carbon and nitrogen have also been used in an attempt to reconstruct the diet of a few Neandertals and some anatomically modern humans. In a study of the strontium levels in bones of Neandertals from Tabun and early modern humans from Skhul and Qafzeh, Schoeninger (1982) concluded that these two groups consumed considerable amounts of meat.

These limited isotopic analyses are not sufficient to provide a clear picture of the Neandertal dietary habits, but they make it possible to identify marine from terrestrial animals, herbivores from carnivores, and browsers from grazers (Figure 4). Although these studies may distinguish between species at the level of broad dietary categories, they do not permit the detection of subtle differences in diet. Another complicating factor is that different combinations of foods can sometimes give similar carbon and nitrogen isotopic ratios. Finally, bone and enamel appetite is easily altered by postmortem diagenesis (Lee Thorp et al. 1989). Thus, the information obtained from these studies is very valuable, but is still limited. While additional stable isotope data may well speak to the general dietary proclivities of Neandertals, it is doubtful that these studies alone will resolve questions about possible dietary differences among Neandertal groups that existed under different environmental conditions. Whenever possible, however, the stable isotope data should be used as complementary to the occlusal microwear data for dietary reconstructions of the Neandertals.

Biochemical inversion method

In a recent study, Balter and Simon (in press) use a new method, the biochemical
data inversion method, for the reconstruction of the diet of the Saint Césaire Neandertal.
This method uses the strontium-calcium (Sr/Ca), barium-calcium (Ba/Ca) and carbon-
nitrogen data of the Neandertal and the associated fauna, along with available Sr, Ba and
Ca contents of plants, to infer the composition of the diet of the Saint Césaire Neandertal.
The results of this study indicate that meat formed 97% of the diet of this individual, and
that plants were almost nonexistent in the diet (Balter et al. 2001; Balter and Simon in
press). When considering the entire faunal assemblage as the dietary source, the
calculation shows that meat was obtained from several species with bovid meat being the
most abundant (58%) followed by the meat of horses/rhinoceros (22%), reindeer (13%),
and mammoth (7%) (Balter and Simon in press).

Buccal microwear analysis

Neandertal diet has been studied also by looking at the microwear on the buccal
sides of the molars and the labial aspects of the anterior teeth (Lalueza and Pérez-Pérez
1993; Lalueza et al. 1993; 1996; Pérez-Pérez et al. 1999; 2003). Buccal microwear
features have been argued to be related to the consistency of the food eaten and the
amount of abrasive particles present in humans and nonhuman primates (Lalueza and
Pérez-Pérez 1993; Lalueza et al. 1993; Lalueza et al. 1996; Pérez-Pérez et al. 1994;

Puech and Pant 1980). These features might also be caused by abrasive particles of sand, dust and ashes which are sometimes ingested with the food (Pérez-Pérez et al. 1999; Pérez-Pérez et al. 1994).

Buccal microwear was examined on the teeth of 68 Paleolithic specimens from Europe and the Levant and modern human groups with known diets (Lalueza and Pérez-Pérez 1993; Lalueza et al. 1993; Pérez-Pérez et al. 2003). The modern groups were divided into mixed-diet hunter-gatherers (Andamanese and Veddahs from tropical forest environment, and Bushmen, Austrialian Aborigines and Tasmanians from arid and mesothermal environments), canivorous hunger-gatherers (Fueguans, Inuit, Vancouver Islanders and Lapps), and agriculturalists (Hindu sample). These studies reported significant differences in the buccal microwear pattern among the modern groups. The buccal microwear analyses suggest that the Neandertals, as a group, had a diet more similar to that of modern hunger-gatherers than to those of agriculturalists or pastoralists (Lalueza et al. 1996). Lalueza et al. (1993; 1996) and Lalueza and Pérez-Pérez (1993) also suggested that Tabun 1, Tabun 2, Amud 1 and La Quina 5 Neandertals had diets similar to those of modern hunter-gatherers with high levels of meat consumption (i.e., Fuegians, Inuit), whereas the diet of Neandertals from St. Cesaire, Malarnaud and Marillac was closer to modern hunter-gatherers who had a mixed-diet (i.e., Andamanese, Kalahari San). This later category was also said to characterise the Qafzeh and Skhul fossils and the archaic and the Upper Paleolithic sample (Abri-Pataud, Cro-Magnon 4, La Chaise Burgeois et Delauney, La Chaise Suard, La Madelaine, Montmaurin, and Rond-du-Barry). Lalueza et al. (1996) suggest that the differences in the diet of the Neandertals may be a result of their geographical and temporal diversity. Pérez-Pérez et al. (2003)

concluded that Neandertals were not strictly carnivorous, but that they also included plant

foods in their diets, since their buccal microwear pattern was highly heterogeneous

compared to those of Middle Pleistocene and early Upper Paleolithic human groups.

Therefore, to explore this further, Pérez-Pérez et al. (2003) divided the Neandertal sample

by cold and warm periods. They found that the specimens from the glacial times of OIS

4 had higher mean densities of striations than those from the warmer periods of OIS 5

and OIS 3. Thus, they concluded that during cold periods, Neandertals relied on hard

plant food intake whereas during warm episodes they had a less abrasive diet, perhaps

including more meat. However, the authors fail to note that their results also show that

the microwear patterns of the Neandertals they sampled from the glacial of OIS 6 had the

lowest mean striation density among all the fossil groups analyzed. This is clearly in

contradiction with their suggestion that during colder times the Neandertals relied on

more abrasive foods.

Although buccal microwear has been shown to differ significantly between

modern human groups with different diets, information about the variability of the

striation patterns on the buccal surface is still relatively limited, and the causative factors

behind these patterns are not well understood (Lalueza and Pérez-Pérez 1993; Lalueza et

al. 1993; Pérez-Pérez et al. 1999; Pérez-Pérez et al. 1994). Its application to fossil

species is, therefore, questionable. This study will test whether the differences in buccal

microwear among the modern human groups analyzed by Lalueza et al. (1996)

correspond to those detected using occlusal microwear analysis.

Chapter 4

Occlusal Microwear Analysis

History of research

Occlusal dental microwear analysis has been shown to have the potential to reveal slight differences in the diets of closely related species (El Zaatari et al. 2005; Teaford 1985; Teaford and Glander 1991; Teaford and Robinson 1989). Occlusal microwear has been examined in a variety of extant (from living animals and museum collections) species in order to infer jaw movements and/or diet (El Zaatari et al. 2005; Gordon 1982; 1984a, b, c; Peters 1982; Ryan 1981; Taylor and Hannam 1987; Teaford 1985; Teaford 1986; Teaford and Glander 1991; Teaford and Oyen 1989a, b; Ungar 1994; Walker 1980; Walker 1981). Studies of dental microwear are based on the analyses of percentages and dimensions of micowear features (pits and scratches) on the tooth surface caused by different factors. These factors can be attributed to characteristics of the abrasives ingested with the food (Daegling and Grine 1999; Teaford and Glander 1991), to the enamel microstructure (Maas 1991), and to the properties of jaw biomechanics (Gordon 1982). However, studies of extant animals have shown that the mechanical properties of the diet itself are considered to be the primary cause of these patterns. For extant primates with known diets, studies of molar microwear have shown that a diet of harder objects, such as hard seeds and nuts, results in heavily pitted surfaces, a diet of grasses or leaves results in heavily scratched ones, and that a mixed diet, or a diet consisting of

foods with intermediate properties, lead to intermediate microwear patterns (Harman and Rose 1988; Marks et al. 1985; Rose 1984; Rose and Marks 1985; Teaford 1988; Teaford and Oyen 1989a; Teaford and Walker 1984).

Early dental microwear studies inferred diet using qualitative observation from binocular light microscopy. These studies were able to show that differences in microwear could be related to dietary/behavioral differences (e.g., Baker et al. 1959; Butler 1952; Walker 1976). By the late 1970s, the scanning electron microscope (SEM) replaced the light microscope (e.g., Ryan 1980; Walker et al. 1978) and, soon after, the quantification of microwear features began to be performed (e.g., Gordon and Walker 1983; Kay and Covert 1983; Peters 1982). The use of quantitative techniques allowed for greater objectivity and the standardization of methodology.

Specimen preparation

Because of the difficulty, if not impossible of transporting actual dental remains from museums to the labs where microscopy is conducted, high-resolution casts of these teeth are prepared and examined instead. After the occlusal surfaces are cleaned, a silicon-base molding material, Polyvinylsiloxane regular body President microSystemTM (*Coltène*®), is usually used for making the molds of the teeth. Epoxy resin is poured into the molds and left to harden. The replicas are then sputter-coated with gold or silver and mounted on stubs if they were prepared for SEM examination. No coating is required for examination under white light confocal profiler.

The quantitative techniques used most extensively for dental microwear analysis were developed by Teaford and Walker (Teaford 1985; Teaford and Walker 1984), Grine (1986), and Ungar (1995). All three methods utilize the scanning electron microscope to record micrographs of occlusal wear facets. Microwear features were identified and measured by defining the four points that identified the long and short axis of each feature. However, these methods differ in the SEM settings used to take the micrographs, the number of micrographs used, the method of measuring features and the definition of feature density. Teaford and Walker's technique (Teaford 1985; Teaford and Walker 1984), used two micrographs for each facet taken at a magnification of 500x using 25 kV in the secondary electron mode. Then, using a digitizer, the 4″ x 5″ contact prints of the micrographs are measured. Feature density was defined as the total number of visualized features on the micrograph (including features whose margins have been truncated by the edges of the image). Finally, the data from the two micrographs are averaged to produce a single value for each variable. Grine's (1986) methodology recorded two micrographs for each facet, with one of them at a magnification of 100x and the second at 200x. Both micrographs were taken using 10 kV in the secondary electron mode. Both 4″ x 5″ negatives were then printed at 8″ x 10″; the 100x print is used to determine feature numbers while the 200x print is used to determine feature diameters. Features are measured and recorded using an S-A Graf-pen sonic digitizer and digital calipers with tapered ends. Truncated features are not measured. Ungar's (1995) technique uses two micrographs for each specimen taken at 500x magnification using 20 kV in a back-

scattered electron mode. The 4″ x 5″ contact prints were then scanned and cropped to a

480 x 640 pixel image. Using a semiautomated procedure and his MICROWARE

software, all features, including truncated ones, on each image were identified and four

points identifying the long and short axis of each were marked by the observer by means

of a mouse driven cursor. Feature measurements were automatically recorded by the

MICROWARE software.

Microwear texture analysis

Each of the conventional methods of dental microwear analysis has its limitations.

In spite of their success, these methods are still at least partly subjective, time-consuming,

and costly. As a result, researchers have been searching for ways to develop the field of

dental microwear to obtain more objective and directly comparable results. A new

approach to the study of dental microwear has been presented recently by Ungar et al.

(2003). This technique, known as microwear texture analysis (described in detail in

Chapter 6), replaces the SEM with finconfocal microscopy and introduces scale-sensitive

fractal analysis as a tool for the analysis of microwear features. Microwear texture

analysis has proven to be as effective as the conventional microwear methods in

separating extant primate species by dietary habit while bypassing the limitations

encountered by these methods (Scott et al. 2005, 2006). In comparison to more

traditional techniques of microwear analysis, microwear texture analysis offers three-

dimensional images of the surface, which provide a more realistic and reliable

representation of the tooth surface. SEM images are greatly affected by different

instrumental settings (such as collector type and position, types of electrons used, voltage, working distance, surface tilt, orientation of the light source) that can lead to different images of the same surface. Thus, microwear texture analysis increases consistency and repeatability of surface measurements. Repeatability of measurement is further enhanced by eliminating the observer subjectivity involved in the process of data collection when using the traditional methods. With all previous microwear analysis techniques, including the semiautomated one, subjectivity in identifying features and their boundaries leads to a high inter-observer and intra-observer error rates which were calculated to be 9% and 7% respectively (Grine et al. 2002). This has been a major problem in the comparison and combination of dental microwear data collected by different observers. This, however, is not the case with microwear texture analysis because measurements are done automatically, without observers interference. Automated data collection is also less time-consuming, because it does not require manually marking the boundaries of each feature on a micrograph. Finally, the operational costs of the SEM are very high compared to those of the confocal microscope. The former requires special specimen preparation procedures (gold or silver coating, mounting, etc.), whereas the latter requires only a standard white-light bulb and does not necessitate any specific specimen preparation. These factors combine to enable significantly larger samples to be analyzed in a comparable time by microwear texture analysis. For these reasons, microwear texture analysis was the method employed in this study.

Chapter 5

Materials

The fossil sample

Dental microwear data were collected from a total of 54 permanent molars attributed to Neandertal, Pre-Neandertal and early Upper Paleolithic specimens. One molar (either M1 or M2) was selected to represent each individual. There is a possibility that the microwear signature might differ between M1 and M2 due to the fact that M2 is closer to the temperomandibular joint (Gordon 1982). The use of both teeth is expected to increase the variation within the samples. However, due to the small sample sizes of the fossil groups, analysis could not be restricted to only one tooth. Therefore, to reduce the possible effect of analyzing teeth from different positions, both M1 and M2 were included in the modern comparative samples. Only molars of adult individuals were included in this study. These specimens derive from 28 sites that cover various parts of Europe and the Middle East (Figure 5), and from oxygen isotope stages 18 through 3, spanning some 700 kyr from c. 735 to c. 24 kyr. Information on site locations, dates of the fossils, reconstructions of the climate and vegetation cover of the areas of the sites during the time of accumulation of these fossils, and specimen attributions of all the fossils examined are discussed below and summarized in Table 3. Whenever available, information on the dietary habits of these specific fossils and the archaeological complex with which they are associated are also included. The specimens are organized by age.

Mauer

Specimens examined

      The lower right molars (M1-M3) of the Mauer mandible were examined and microwear data were collected from the RM_2. A cast of this specimen was provided by A. Pérez-Pérez.

Site location

      The mandible was found at the Rösch sand quarry in the village of Mauer, some 16 km southeast of Heidelberg, Germany

Date

      Faunal analysis places the Mauer mandible between the Cromerian and Holsteinian interglacials (OIS 13) which makes it around 500 kyr old (Cook et al. 1982). However, the dating of the geological layers in which the jaw was found indicates that it is older than 500 kyr, and probably between 735-640 kyr in OIS 16-18 (Hambach 1996; Hambach et al. 1992).

Climate/Vegetation cover

      No direct evidence from the Mauer site is available for the climatic conditions at the time of deposition of the mandible, but climatic conditions can be inferred from the reconstructions based on the oxygen isotope values of contemporary deep sea cores

(Figure 3). Glacial conditions prevailed during OIS 16-18, and it appears that even at the peak of OIS 17, conditions were similar to those of glacial rather than interglacial times. During glacial times, central Europe was covered with steppe/tundra vegetation (Figure 2).

<u>Attribution</u>

Homo heidelbergensis (Tattersall 1986).

Arago

<u>Specimens examined</u>

Casts of molars representing five Arago specimens (Arago 2, 5, 13, 21 and 54) were provided by A. Pérez-Pérez for the purposes of this analysis. Those of Arago 2 and 5 were found to be too poorly preserved for microwear analysis and were thus excluded from this study. Microwear data were collected from the RM_1 of Arago 13, the RM^1 of Arago 21, and the RM_1 of Arago 54.

<u>Site location</u>

This cave site is located in Verdouble River valley, between the towns of Tautavel and Vingrau in southern France.

<u>Date</u>

The layer which yielded the human fossils is dated to 410-450 kya (Iacumin et al. 1996). The same age was obtained from direct U-series dating on Arago 21, but this date had a very wide margin of error (Yokoyama and Nguyen 1981).

Climate/Vegetation cover

Climatic reconstruction suggest cold and dry conditions at the time of accumulation of the Arago hominin remains, and that the landscape was open and covered mainly by grass, corresponding to Arctic tundra or a cold arid steppe conditions (de Lumley et al. 1984).

Archaeological association

Tayacian (Schwartz and Tattersall 2002).

Attribution

Homo heidelbergensis (Rightmire 1990; Stringer and Gamble 1993; Tattersall 1986; Tattersall 1995)

Steinheim

Specimens examined

The RM[1] of Steinheim 1 was included in the current study. The molars of the Steinheim skull were molded at the Staatliches Museum für Naturkunde, Stuttgart, Germany.

This skull was found in a gravel quarry in Steinheim, about 20 km from Stuttgart, Germany.

Date

Associated faunal remains date to interglacial times, either to the Holstein (Vlcek 1991), which is correlated with OIS 9 (around 325 kyr), or to the Penultimate interglacial, correlated with OIS 7 at about 225 kyr (Adam 1985).

Climate/Vegetation cover

Associated fauna indicates a woodland environment during the time of its deposition (Adam 1954).

Attribution

There is general agreement that this specimen displays some Neandertal apomorphies and that it belongs to a pre-Neandertal or early Neandertal group (Dean et al. 1998).

Atapuerca – Sima de los Huesos

Specimens examined

Casts of molars representing 12 individuals were provided by A. Pérez-Pérez for this analysis. The occlusal surfaces of the molars of five of these (6, 11, 12, 26, and 27) showed signs of taphonomic damage and were excluded from this analysis. Microwear data were successfully collected from molars representing the seven remaining individuals: 3 (RM^2), 4 (RM^1), 7 (LM^2), 8 (RM^1), 17 (RM^1), 19 (LM^2), and 22 (RM^1).

Site location

These remains were found in a vertical shaft within Cueva Mayor in Sierra de Atapuerca cave systems, east of Burgos, Spain.

Date

ESR and U-series dating suggest an age of between 300-200 kyr (Bischoff et al. 1997; Falguères et al. 2001). The paleomagnetic evidence supports this age (Parés et al. 2000), although more recent U-series dating suggests that these remains are older than 350 kyr, with a possibility they date to between 400-600 kyr (Bischoff and Shamp 2003).

Climate/Vegetation cover

Palynological samples taken from the matrix of the human fossils are composed by about 40% by pollen of the pine tree Pinus, with deciduous oak, and evergreen oak, birch and *Fagus* in decreasing order of abundance (García-Antón 1987).

Dietary habits

An analysis of enamel hypoplasia showed that 4.6% of the teeth were affected, which has been interpreted to mean that this sample experienced a low level of developmental stress (Cunha et al. 2004).

Attribution

Homo heidelbergensis (Arsuaga et al. 1997).

Pontnewydd

Specimens examined

Two isolated molars, Pontnewydd 1 (RM^2) and 12 (LM^1) representing two individuals were examined. Casts of these specimens were provided by A. Pérez-Pérez.

Site location

This cave site lies in the Elwy Valley, on the western edge of Vale of Clywd, around 6 km northwest of the town of Denbigh, England.

Date

TL dates place the fossils at 200 ±25 kyr (Green et al. 1981)

Climate/Vegetation cover

Faunal association suggests interglacial conditions (Green 1983) and TL dating places the teeth within the last substage of OIS 7 or OIS 7a. Reconstructions of the

vegetation cover during these times indicate that the area was covered by conifer forests

(Turner 1975).

Attribution

The Pontnewydd remains are attributed to "archaic" Neandertals (Green 1981).

They are thus grouped with the Pre-Neandertals for the purposes of this study.

Archaeological association

The teeth were associated with Acheulian artifacts (Green 1981).

Montmaurin

Specimens examined

Molars of the single adult mandible from Montmaurin were examined and

microwear data were collected from the RM_1. Casts of this specimen were provided by A.

Pérez-Pérez.

Site location

This cave site is located at the foothills of the Pyrenees in the valley of Seygouade

River at Montmaurin, southern France.

Date

The specimen most likely dates to the end of the Riss glaciation, around 130 kyr (Girard and Renault-Miskovsky 1983).

Climate/Vegetation cover

Pollen analysis suggests that the environment was relatively open, with trees comprising only 20% of the vegetation. Pine trees interrupted the spread of vast herbaceous areas, and this is characteristic of a relatively cool and humid climate (Girard and Renault-Miskovsky 1983).

Attribution

Pre-Neandertal (Howell 1960; Vallois 1955; Vallois 1956).

Archaeological association

This fossil was found in a pre-Mousterian context (Vallois 1956).

Tabun

Specimens examined

The RM^1 of Tabun I (C1) and and LM_2 of Tabun II were included in this study. Molds of the dental remains of Tabun 2 were provided by Y. Rak, and those of Tabun 1 were obtained at the British Museum of Natural History, London, UK.

Site location

This cave site is located on Mt. Carmel, 20 km south of Haifa, Israel.

Date:

The stratigraphic location of the Tabun I specimen is still debated. The controversy is whether this specimen came from layer B or C (Alperson et al. 2000; Bar-Yosef and Callander 1999; Garrod and Bate 1937; Schwarcz et al. 1998). Tabun II comes from level C, which has been dated by ESR to between 120 ±16 kyr and 140 ±21 kyr (Grün and Stringer 2000), and by TL on burnt flint to some 165 ± 16 kyr (Mercier and Valladas 2003). Direct U-series and ESR dating on the C1 skeleton provide dates of 34 - 33 kyr and 40 kyr respectively (Grün and Stringer 2000; Schwarcz et al. 1998). However, these early dates are considered by many to be unreliable (Alperson et al. 2000; Millard and Pike 1999). Thus, Level C is considered here to date between 165 and 120 kyr. Level B is dated by ESR to between 102 ±17 and 122 ±16 kyr (Grün and Stringer 2000).

Climate/Vegetation cover

The dates available for the Tabun remains cover OIS 6 and OIS 5. Climatic reconstructions indicate that during OIS 6 the Levant was covered by semi-desert vegetation, whereas during OIS 5e it was covered by a Mediterranean evergreen woodland (see Chapter 2 for detailed discussion). In OIS 5b and 5c there was a mix of Mediterranean evergreen woodland and deciduous forest and in OIS 5d and 5b there was an increase of open vegetation.

Attribution

Neandertal (Garrod and Bate 1937).

Archaeological association

Mousterian (Jelinek 1981).

Saccopastore

Specimens examined

Microwear data were collected from the LM^2 of Saccopastore 1 and RM^2 of Saccopastore 2s. These remains were molded at the Dipartimento di Biologia Animale e dell'Uomo, Universita' di Roma "La Sapienza", Rome, Italy.

Site location

These fossils were found in a gravel pit in the suburbs of Rome, Italy.

Date

There is a general agreement that these specimens date to OIS 5e, around 130-120 kyr (Blanc 1957; Condemi 1992).

Climate/Vegetation cover

During OIS 5e, this part of Italy was covered by Mediterranean evergreen woodland (see Chapter 2).

Neandertal (Sergi 1935; Sergi 1948).

Archaeological association

Pontian Mousterian (Blanc 1939a).

Guattari

Specimens examined

The RM_2 of the Guattari 3 mandible was included in this analysis. This specimen was molded at the Dipartimento di Biologia Animale e dell'Uomo, Universita' di Roma "La Sapienza", Roma, Italy.

Site Location

This cave site lies in the southeastern side of Monte Circeo, Italy.

Date

U-series and ESR dates indicate an age of between 60-74 kyr (Grün and Stringer 1991; Schwarcz et al. 1991a; Schwarcz et al. 1991b).

Climate/Vegetation cover

The area around Guattari during this time was covered by an arid cold steppe vegetation (see Chapter 2).

<u>Attribution</u>

Neandertal (Blanc 1939b; Blanc 1951; Sergi 1935).

<u>Archaeological association</u>

Pontinian Mousterian (Taschini 1979).

Subalyuk

<u>Specimens examined</u>

The LM$_2$ of Subalyuk 1 mandible was examined for this study. The lower left

molars of this mandible were molded at the Hungarian Natural History Museum,

Budapest, Hungary.

<u>Site location</u>

This is a cave site located near the village of Cserepfalu, Borsod County, northern

Hungary.

<u>Date</u>

Microfauna date the fossil to around 70-60 kya (Schwartz and Tattersall 2002).

<u>Climate/Vegetation cover</u>

The microfauna are strongly indicative of a continental steppe climate (Schwartz and Tattersall 2002).

Attribution

Neandertal (Szabo 1935).

Archaeological association

Eastern Moursterian (Kadic 1940).

Kebara

Specimens examined

The LM_2 of Kebara 2 was included in this study. Molds of this specimen were provided by Y. Rak.

Site location

This is a cave site located on the western slopes of Mt. Carmel, around 30 km south of Haifa and 2.5 km east of the Mediterranean in Israel.

Date

TL provides a date of 59.5 ±3.5 kyr (Valladas et al. 1987), and ESR dating gives it a similar age of 64-60 kyr (Schwarcz et al. 1989).

<u>Climate/Vegetation cover:</u>

Reconstructions for the period between 64-60 kyr place Kebara 2 in a transitional period between OIS 4 and 3. Semi-desert vegetation prevailed in this area of the Levant at the peak of OIS 4, around 65kyr (see Chapter 2). However, the period at the beginning of OIS 3 (around 60 kyr) witnessed an increase in tree cover in response to a short warm episode. Thus, because we do not have a more accurate date for this fossil, and given the short term, but sharp oscillations during OIS 3, it would seem best to describe the vegetation at the time as an expansion of woodland in a mainly semi-desert landscape (Cheddadi and Rossignol-Strick 1995).

<u>Dietary habits</u>

Analysis of the faunal assemblage from Kebara suggest that the Neandertals hunted prime adults of gazelle, fallow deer, red deer, wild boar, equids and aurochs in this order (Speth 2002). There is evidence that tortoise presented an important food source for the Neandertals at Kebara (Speth 2002). Charred seed remains broad-spectrum plant foraging, with Legumes being the most abundant (Lev et al. 2005).

<u>Attribution</u>

Neandertal (Bar-Yosef et al. 1992).

<u>Archaeological association</u>

Mousterian (Bar-Yosef et al. 1992).

Amud

Specimens examined

 The RM_2 of Amud I was examined in this study. Molds of the Amud I specimen were provided by Y. Rak.

Site location

 This cave site is located in Wadi Amud, 10km north of the town of Tiberias, 50 km east-north-east of Haifa, Israel.

Date

 TL on burnt flint suggest a date of around 55 kyr (Valladas et al. 1999). ESR and Th/U dates on associated faunal teeth date the Amud I layer to 53 ±8 kyr (Rink et al. 2001).

Climate/Vegetation cover

 The period at the beginning of OIS 3, between 58 and 54 kyr, was relatively warm. The vegetation during this period was most likely similar to that of the period between 39-36 kyr (van Andel and Tzedakis 1996), when the Levant was covered by a mix of coniferous and deciduous forest (van Andel and Tzedakis 1996).

Dietary habits

Analysis of phytoliths from the Amud sediments indicates that the inhabitants of the site were exploiting palm and figs (Madella et al. 2002). There is also evidence that seeds were collected (Madella et al. 2002). The fauna is dominated by gazelle, fallow deer, wild goat, red deer, roe deer, aurochs, wild boar and rhinoceros (Rabinovich and Hovers 2004).

Attribution

Neandertal (Howells 1974; Stringer 1974).

Archaeological association

Mousterian (Suzuki and Takai 1970).

La Quina

Specimens examined

The RM^2 of La Quina 5 and LM^2 of La Quina 20 were examined. The casts of the La Quina 5 dental remains were provided by A. Pérez-Pérez, whereas the dental remains of La Quina 20 were molded by me at the Musée des Antiquités Nationales, St. Germain-en-Laye, France.

Site location

La Quina is a rock-shelter located in southwestern France, near Villebois-Lavaletter which is 25 km south of Angoulème, Charente, France.

Two Carbon-14 dates for bed 3, from which the La Quina 5 fossil was recovered, indicate 31,100 ±400 and 34,100±700, with the latter being considered more reliable (Vogel and Waterbolk 1967).

Climate/Vegetation cover

Pollen from bed 3 shows an increase in arboreal species compared to the older levels, indicating that the climate was milder and more humid (Renault-Miskovsky 1998). Arboreal pollen increased gradually from 5% at the beginning of this layer to around 20% at its top. There is also a large increase in the percentage of ferns in this level and an overall increase in plants that prefer moist conditions (Renault-Miskovsky 1998). However, steppe taxa still dominated the assemblage. Among the trees, conifers dominate, but some deciduous taxa were present (Renault-Miskovsky 1998). Pollen analysis indicate that the vegetation was mostly steppic, but interrupted by coniferous and, to a lesser extent, deciduous trees.

Dietary habits

Studies of plant remains suggest that the Neandertals from La Quina exploited a variety of soft and hard plants, and wood (Hardy 2004). Evidence of the exploitation of mammals and birds were also found on associated stone tools (Hardy 2004).

Attribution

Neandertal (Henri-Martin 1923).

Mousterian (Henri-Martin 1923)

Sidrón

Specimens examined

The LM_1 of Sidrón 1 and the LM_2 of Sidrón 2 were included in this study. Casts of these specimens were provided by A. Pérez-Pérez.

Site location

This cave is located in Piloña, Asturias, northern Spain.

Date

Caliberated radiocarbon dates place these remains between 42-44 kyr (Lalueza-Fox et al. 2005).

Climate/Vegetation cover

Pollen sequences from the cores in the Atlantic Ocean and Alboran Sea around the Iberian Peninsula show that, with the exception of a short period around 43.7 kyr, the vegetation between 42 and 44 kyr was dominated by temperate taxa (d'Errico and Sánchez Goñi 2003; Genty et al. 2005). Pine is the most dominant species in the pollen

spectrum (Roucoux et al. 2005), and the second most common tree species was the deciduous oak (Roucoux et al. 2005). The percentage of pollen from steppic plants was relatively low, fluctuating between 20 and 30% (d'Errico and Sánchez Goñi 2003). Thus, it can be concluded that the vegetation at the time of deposition of the Sidrón fossils was coniferous and deciduous woodland.

Attribution

Neandertal (Fortea et al. 2003).

Vindija

Specimens examined

The molars of following specimens from Vindija cave were examined 11.39 (RM_1), 11.45 (L M_2), 11.46 (LM^1), 11.409 (LM_1), 12.1 (RM^2). Casts of these specimens were provided by A. Pérez-Pérez.

Site location

This cave is located close to the center of Ivanec, 55 km from Zagreb, Croatia.

Date

These specimens were recovered from level G3. C14 dates on bear and hominin bones date level G3 to 42 kyr (Ahern et al. 2004).

Climate/Vegetation cover

Pollen analyses from ODP 976 core show that at 42 kyr, the vegetation was dominated by temperate taxa (Genty et al. 2005). La Grande Pile also shows similar results (Woillard and Mook 1982).

Dietary habits

Carbon and nitrogen stable isotope analysis suggests that the Vindija hominins were top-level carnivores (Richards et al. 2000).

Attribution

Neandertal

Archaeological association

Mousterian.

Spy

Specimens examined

The RM^2 of Spy 1 was included in this study. Casts of the dental remains of Spy 1 are available at the Anthropology Department at Stony Brook University. These remains were molded by Peter Ungar.

Site location

Spy is a cave site located in the limestone bluff of Betche-aux-Roches near the village of Spy, some 15 km from Namur, Belgium.

Date

The Spy remains most probably date to between 35-40 kyr based on faunal association (Cordy 1988).

Climate/Vegetation cover

The period between 39-36 represents one of the warm episodes during OIS 3 (see Chapter 2). This area of northern Europe was covered by a shrub tundra vegetation during the time that the Spy Neandertals inhabited the site.

Attribution

Neandertal (Fraipont and Lohest 1887)

Archaeological association

Mousterian (Cordy 1988).

Grotta Breuil

Specimens examined

The isolated LM_1 of Breuil 2 (Manzi and Passarello 1995) has been analyzed. This fossil was molded at Dipartimento di Biologia Animale e dell'Uomo, Universita' di Roma "La Sapienza", Rome, Italy.

Site location

Breuil is a cave site in the limestone cliffs of Monte Circeo, a promontory on the Tyrrhenian coast of central Italy.

Date

ESR dating on mammal teeth provided a date of 37 kyr (Schwarcz et al. 1991b).

Climate/Vegetation cover

This fossil comes from a temperate climate (Recchi 1995). At 37 kyr, it falls during a warm phase in OIS 3. Reconstructions of the vegetation cover indicate that this area had deciduous woodland vegetation (see Chapter 2).

Dietary habits

There is evidence of human accumulation of *Cervus elaphus, Capra ibex, Bos primigenius, Capreolus capreolus, Equus hydruntinus* (Stiner 1991).

Attribution

Neandertal (Manzi and Passarello 1991; Manzi and Passarello 1995).

Pontinian (Mousterian from the sites of the Circeo promontory) (Bietti et al. 1991)

Saint Césaire

Specimens examined

The St. Césaire 1 RM[1] was included in this analysis. The molars were molded at the Musée des Antiquités Nationales (St. Germain-en-Laye), France.

Site location

This site is a rock-shelter located beside the Coran River in the village of St. Césaire, 12 km east of Saintes, Charente-Maritime, France.

Date

TL dates on burnt flint from the Châtelperronian provide an age of 36.5 ±2.7 kyr (Mercier et al. 1991).

Climate/Vegetation cover

Reconstructions of the vegetation cover for this period indicate that the area of St. Césaire was covered by an open coniferous forest (see Chapter 2).

Dietary habits

Analysis of Sr/Ca and Ba/Ca ratios of the St. Césaire specimen suggest that its diet was mainly carnivorous, with meat forming around 97% in weight of consumption (Balter et al. 2001). The carbon-nitrogen isotope analysis suggests that the St. Césaire individual fed primarily on the meat of herbivore, and that this came mostly from the large species (Bocherens et al. 2005).

Attribution

Neandertal (Lévêque and Vandermeersch 1980).

Archaeological association

This fossil was recovered from a Châtelperronian context (Lévêque and Vandermeersch 1980).

Zafarraya

Specimens examined

The RM_1 of the Zafarraya mandible was examined. Casts of this specimen were provided by A. Pérez-Pérez.

Site location

This karst cave is located in Sierra de Alhama in Alcaucin, in the northeastern extremity of the province of Malagá, Spain.

Date

U-series dates on animal bone and teeth in association with the fossil provide an age of 33.4 ±2 kyr for this specimen (Hublin et al. 1995).

Climate/Vegetation cover

The flora of the Zafarraya deposits suggest that the most common tree was oak (Barroso Ruiz et al. 1984). 33 kyr marked the beginning of a cold event in OIS 3. Pollen analyses from the OPD 976 and MD95-2043 cores located in the Alboran Sea indicate that at this time pollen from semi-desert taxa was relatively low, around 20-30% (d'Errico and Sánchez Goñi 2003; Genty et al. 2005). Thus, the vegetation during the time of deposition of the Zafarraya mandible was relatively wooded.

Attribution

Neandertal (Garcia Sanchez 1986).

Archaeological association

Mousterian (Barroso Ruiz et al. 1983; Barroso Ruiz et al. 1984).

Ochoz

Specimens examined

The LM_2 of the Ochoz 1 mandible was included in this analysis. Casts of this specimen were provided by A. Pérez-Pérez.

This cave site is located southwest of the Ochoz village, 35 km north of Brno, Moravia, Czech Republic.

Date

This fossil dates either to last interstadial (OIS 3) or the last interglacial (OIS 5) (Schwartz and Tattersall 2002).

Climate/Vegetation cover

This fossil comes from interglacial times, but because there is no paleoclimatic reconstruction, from the site itself, and since the site is not properly dated, it is impossible to infer climatic conditions for it.

Attribution

Neandertal (Jelinek 1962; Klima 1962; Vanura 1965).

Archaeological association

Mousterian (Vlcek 1991).

Skhul

Specimens examined

Of the three Skhul individuals (Skhul 5, 6, and 7) available for analysis only the dental remains of Skhul 7 yielded good microwear preservation to be included in this study. Microwear data were collected from the LM$_2$ of Skhul 7. Casts of these specimens were provided by A. Pérez-Pérez.

Site location

This cave site is located in Wadi el Mughara Mt. Carmel, southeast of Haifa, Israel.

Date

ESR dates from faunal teeth fall between 81 ±14 kyr and 101 ±12 kyr (Stringer et al. 1989), U-series dates on faunal teeth range from 46 tp 88 kyr (McDermott et al. 1993), and TL values from burnt flint indicate 119 ±18 kyr (Mercier and Valladas 2003).

Climate/Vegetation cover

All of these dates place the Skhul fossil in OIS 5. The Levant was covered by a mix of Mediterranean evergreen woodland and coniferous forest during OIS 5a and 5c (see Chapter 2). The area wittnessed an increase in open vegetation in OIS 5d and 5b, but these never reached glacial levels (see Chapter 2).

Attribution

Archaic *Homo sapiens*.

Lavalloise-Mousterian

Mladeč

Specimens examined

Microwear data were collected from the four Mladeč individuals with preserved molars. The RM^1 of Mladeč 1, LM^1 of Mladeč 2, LM^1 of Mladeč 4, and LM^2 of Mladeč 8 were included in this analysis. These teeth were molded at the Naturhistorisches Museum, Vienna, Austria

Site location

The cave is located west of the village Mladeč and 4.5 km west of the town of Litovel, northern Moravia, Czech Republic.

Date

`Uncaliberated AMS radiocarbon dates place these fossils at about 31 kya (Wild et al. 2005).

Climate/Vegetation cover

No direct information on vegetation from this area is available, but it could be argued that it would have been similar to that from Dolni Věstonice because these two sites and geographical and temporally close. The pollen analysis at Dolni Věstonice

indicates a forest-steppe environmet with dominance of groups of coniferous trees and to

a lesser extent deciduous ones (Svobodová 1991).

Attribution

Modern *Homo sapiens* (Szombathy 1925).

Archaeological association

Aurignacian (Szombathy 1925).

Vogelherd (Stetten)

Specimens examined

The RM$_2$ of the single partial mandible of individual 1 was included in this study.

A cast of this specimen was provided by A. Pérez-Pérez.

Site location

This cave site is located on the eastern rim of the Lone River valley, near Stetten

village, in southwestern Germany.

Date

Radiocarbon dates of the layer V that yielded this fossil are between 30.2 ±13 kyr

and 31.9 ±11 kyr (Churchill and Smith 2000)[4].

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[4] New data suggests that this specimen might date to the Neolithic period (Conard et al., 2004). Thus, the results from this specimen should be viewed with caution.

Climate/Vegetation cover

The pollen sequence from La Grande Pile in France, indicates that the period between 30-28 kyr was an open pine-birch forest (Woillard 1978a; Woillard and Mook 1982). This reconstruction can be used to describe the vegetation cover at Vogelherd at the time of deposition of the Stetten 1 individual because these two sites are in close proximity.

Attribution

Modern *Homo sapiens* (Gieseler 1937).

Archaeological association

Aurignacian (Churchill and Smith 2000).

Combe Capelle

Specimens examined

The RM^2 of Combe Capelle 1 was included in this analysis. This fossil was molded at the Museum für Vor- und Frühgeschichte, Berlin, Germany

Site location

Combe Capelle 1 was found in a rock shelter in the Couze Valley, in Dordogne, southern France.

This fossil was dated by archaeological association to around 28-25 kya (Sonneville-Bordes 1959)[5].

Climate/Vegetation cover

For the short period between 28-25 kyr, the pollen sequence from La Grande Pile reveals an increase in arboreal pollen (Woillard 1978a). The landscape of this period can be described as an open Pine and Birch forest with some other coniferous tree taxa (Woillard 1978a; Woillard and Mook 1982).

Attribution

Modern *Homo sapiens* (Boule and Vallois 1957).

Archaeological Association

Perigordian, which is a phase of the Gravettian.

Předmostí

Specimens examined

The RM$_1$ from the site of Předmostí included in this study is from a mandible (the specimen number is not available) that is one of the very few remains from this site that

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[5] This specimen might have a later date (Hublin, 2006, pers. comm.).

survived destruction during the Second World War. Casts of this specimen were provided by A. Pérez-Pérez.

Site location

Předmostí is an open air site located north of Prerov, northeastern Moravia, Czech Republic.

Date

These remains are radiocarbon dated to around 26 kya (Allsworth-Jones 1986; Svoboda et al. 1994; Vlcek 1991).

Climate/Vegetation cover

Palynological analysis of the Gravettian layer of Předmostí indicates around 31% of the pollen to be arboreal. Since this site is temporally and geographically close to the site of Dolni Věstonice, environmental reconstructions from the later can be used to describe the conditions at Předmostí. These reconstructions suggest that the climate was relatively mild, and that the vegetation was transitional forest-steppe characterized by the abundance of coniferous trees accompanied by deciduous taxa (Svoboda et al. 1994).

Dietary habits

Faunal analysis indicate that people at Předmostí hunted mostly mammoth and complemented this with reindeer, hare, fox, and wolf (Musil 1994).

Modern *Homo sapiens* (Matiegka 1934).

Gravettian (Ullrich 1996).

Pavlov

Specimens examined

The RM$_2$ of the Pavlov 3 mandible was included in this study. A cast of this specimen was provided by A. Pérez-Pérez.

Site location

Pavlov is an open-air site located near the village of Pavlov, southern Moravia, Czech Republic.

Date

Radiocarbon date on charcoal places this fossil around 26 kyr (Klima and Kukla 1963).

Climate/Vegetation cover

Climatic and environmental reconstructions from Dolni Vestonice can be used to describe the conditions at Pavlov because these two sites are close to each other in time

and space. The pollen analysis from Dolni Věstonice indicates a forest-steppe environment with dominance of groups of coniferous trees and to a lesser extent deciduous trees and grasses, sedges and mugworts (Svobodová 1991)

Dietary habits

Analysis of faunal remains suggests that reindeer, fox and hare were hunted (Musil 1994).

Attribution

Modern *Homo sapiens* (Vlcek 1961).

Archaeological association

Pavlovian, which is part of the Gravettian (Klima 1959).

Dolni Věstonice

Specimens examined

Microwear data were collected from: the RM^1 of individual 13, RM_1 of individual 14, LM_2 of individual 16 and RM_1 of individual 31. Casts of these specimens and others corresponding to individuals 3 and 37 were provided by A. Pérez-Pérez. None of the molars of the latter two individuals had good microwear preservation and were, thus, excluded from this study.

These remains were found in an open-air site located on the Pavlovske Hills between the villages of Dolni Věstonice and Pavlov, Czech Republic

Date

Radiocarbon dates place these remains between 29-26 kya (Allsworth-Jones 1986; Svoboda and Vlcek 1991; Vogel and Zagwijin 1967). The triple burial (individuals 13 and 14 here) was radiocarbon dated to 26.64 kya ±110 (Klima 1988).

Climate/Vegetation cover

The pollen analysis indicates a forest-steppe environment with dominance of groups of coniferous trees (Larch and Juniper) and to a lesser extent deciduous (*Qusrcus, Populus* and *Fagus*) trees and grasses, sedges and mugworts (Svobodová 1991). Steppe taxa were also present. This was most likely a transitional environment that has no modern analogue. Overall, it is evident that there was a wide range of plant resources available for the local inhabitants. The analysis of plant macro-remains from the site also support such a climatic and ecological reconstruction (Mason et al. 1994).

Dietary habits

Faunal analysis at the Dolni Vestonice show remains of the following animals in decreasing abundance: mammoth, fox, wolf and reindeer (West 2001). Arctic hare and horse were limited at the site (West 2001). It is not certain if these animals were hunted for food or other purposes.

Modern *Homo sapiens* (Vlcek 1991).

Archaeological association

Gravettian (Vlcek 1991).

Barma Grande

Specimens examined

Microwear data were collected from LM$_2$ of Barma Grande 1, RM$_2$ of Barma Grande 2 and RM^2 of Barma Grande 5. These are the only adult individuals recovered from the early Upper Paleolithic layers of the site. The dental remains of Barma Grande 1 were molded at the Musée de Préhistoire Régionale, Menton, France and those of Barma Grande 2 and 5 were molded at the Museo Preistorico dei Balzi Rossi, Ventimiglia, Italy.

Site location

The Barma Grande cave is part of the Grimaldi Caves of Ligura. These are located at the boarder between France and Italy at the base of the Balzi Rossi cliffs, northwestern Italy.

Date

The triple Barma Grande burial (individuals 2-4) is dated by archaeological association to around 25 kyr (Schumann 1995). AMS ^{14}C provides an age of 26.4-23.2 kyr for the Barma Grande 6 specimen (Formicola et al. 2004). Based on the similarity of grave goods and the proximity of the burials to one another, this can also be considere the date of the rest of the individuals from the site (Formicola et al. 2004).

Climate/Vegetation cover

Pollen analysis from Italian sites (Lago Grande di Monticchio, Lagaccione, Vico and Valle di Castiglione) shows that during the time between 26-23 kyr, the area was covered by open vegetation. Coniferous tree pollen was present in the area, but in relatively low quantities (around 20%) (Follieri et al. 1998; Watts et al. 1996). Similar conditions were also detected in the deep sea cores from the Mediterranean (Genty et al. 2005).

Attribution

Modern *Homo sapiens* (Schumann 1995).

\Archaeological association

Aurignacian (Schumann 1995).

Recent sample

A total of 165 molars (one molar per individual) of 7 modern hunter-gatherer groups were analyzed for comparative purposes. The molars with the best microwear preservation were selected. These groups consisted of Andamanese (n=29), Chumash (n=11), Fuegians (n=6), Alaskans from Point Hope (Ipiutak n=19; Tigara n=24), Aleutian Islanders (n=19), and prehistoric (Khoe-San) hunter-gatherers from South Africa (n=46).

Andamanese

Study sample

The Great and Little Andamans along with other neighboring islands form a volcanic chain that stretches between the province of Pegu and the northernmost point of Sumatra in the Bay of Bengal (Man 1885). The sample of Andamanese included in this study consists of protohistoric specimens dating to the period immediately after the first permanent European settlement of the islands in AD 1958. These dental remains are currently housed at the British Museum of Natural History, London, and belonged to individuals who lived in the area of Port Blair, South Andaman.

Climate

The temperature throughout the year is very uniform. The cool season extends from December to January and the hot season from March to April (Man 1885). The Monsoon extends from April till October (Man 1885). The dry season is accompanied by strong northeastern winds which are usually harmful for vegetation (Man 1885).

<u>Dietary habits</u>

Historic records indicate that the Andamanese relied on marine hunting to provid fish, dugong and sea turtles (Myka 1993). One third of their daily food consumption consisted of edible roots, fruits and honey. They also consumed meat from pig (most frequently hunted in the rainy season), paradoxurus, inguana, turtle, and shellfish (Man 1883). Food was almost always cooked, but eaten half roasted, such that it remained relatively tough (Pal 1984). The food was usually cooked uncovered, which would have enabled contamination by windborne sand (Pal 1984).

Chumash

<u>Study sample</u>

The skeletons comprising this collection were excavated in 1927 from the site of SCrI-3 on the Island of Santa Cruz, one of the four Northern Channel Islands twenty miles off the coast of southern California. This collection dates to between 4000 and 5000 BP (Walker 1986) and is currently housed at the British Museum of Natural History, London.

<u>Climate</u>

Most of the year the climate of this area is predictable. The island chain forms a sheltered channel where moderate winds and air temperatures rarely fluctuate. (Fagan 1995). The area has a Mediterranean climate characterized by cool and wet winters, and warm and dry summers (Kenneth 2005).

The Chumash were fishers and hunters. Their diet was based on fish, marine mammals and other marine resources (e.g., shell-fish). They also ate small terrestrial animals available on the island (Fagan 1995). Isotopic studies show that the Chumash relied heavily on marine protein resources (Walker 1996). Ethnohistoric accounts also indicate that these people relied on several kinds of plants including islay, manzanite, mangle berries, tarweed seeds, tubers and sage (Timbrook 1993; Walker 1996).

Fuegians

Study sample

Tierra del Fuego lies in the southernmost part of South America (Garson 1886). The area has an Antarctic landscape with high mountains (Garson 1886). The skeletons included in this study come from the Museum of Anthropology at the University of Rome. They date to 1880 and come from the Yamana (n=11) and Alakaluf (n=2) tribes (Manzi 1986). These tribes occupied the Beagle Channel islands and the islands of the Chilean archipelago in the south western part of the Tierra del Fuego (Yesner et al. 2003).

Climate

The Beagle Channel has an average summer temperature of 10°C. Average winter temperature can reach -12°C, but the constant winds dramatically increase the

cold. The southern area of Tierra del Fuego is generally forested; however, the temperate forests gradually give way to shrub and tundra towards the south.

<u>Dietary habits</u>

The ethnohistoric record of the late 1800s indicates that the Yamana and Alakaluf tribes of the Chilean archipelago relied on fishing and seal-hunting, although seals rank lower in importance (Bridges 1885; Snow 1861). Guanaco (*Lama guanicoe*) might have also formed a terrestrial source of food (Yesner et al. 2003). Stable isotope analysis of Yamana skeletons indicate that their diet was based on marine resources, but that terrestrial animals formed an important part of their diet as well (Yesner et al. 2003).

Point Hope

<u>Study sample</u>

Point Hope, Alaska, is a peninsula formed by a narrow ribbon of gravel and sand protruding approximately 32 km into the Arctic Ocean some 200 km north of the Arctic Circle. It is the westernmost point of land in Alaska north of the Bering Strait. For the purposes of this study, occlusal molar microwear data were collected from a total of 49 individuals from Point Hope uncovered by excavations between 1939 and 1941. The specimens are currently housed at the American Museum of Natural History. These remains are attributed to two temporally and culturally distinct pre-contact populations: the Ipiutak (n=22; 100 B.C. – 500 A.D.) and the Tigara (n=27; 1200 – 1700 A.D.).

Climate

The Arctic tundra vegetation of Point Hope is characterized by the lack of trees and the presence of moss, lichens, grass and small flowering plants. In winter the peninsula is covered by hard-packed snow, although the ocean currents leave an area of water close to the shore free of pack ice, making Point Hope famous for its great variety of sea mammals (Larsen and Rainey 1948).

Dietary habits

The material culture of the Tigara, suggests that their dietary habits were similar to those of the Point Hope Eskimos who inhabited the area after the European contact (Costa 1980). The diets of the Eskimos living at Point Hope in the 20th century consisted of 35 – 60% fat, 35 – 65% protein and very little carbohydrate (Waugh 1930). The meat component of their diet came mainly of fish, eaten fresh or dried on open racks, whale, eaten fresh or kept frozen underground as a year-round staple, and seal, often eaten raw at the site of the catch or kept frozen (De Poncins 1978; Giddings 1967). Uncooked seal skin together with its attached subcutaneous fat was often chewed for prolonged periods of time (Balikci 1970). Limited carbohydrates came mostly from raw roots (Waugh 1930).

By contrast, the Ipiutak cultural assemblage is predominated by arrowheads in relation to artifacts used for coastal hunting, and lacks artifacts that are typically associated with whaling and that characterize modern coastal Eskimo cultures (Larsen and Rainey 1948). The lack of winter game in the faunal assemblage suggests that the Ipiutak people were seasonal rather than permanent occupants of the coast, following the

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coastal migration of caribou herds in the spring and summer (Larsen and Rainey 1948; Lester and Shapiro 1968). The excavations at the coastal Ipiutak site show that during the summer, they subsisted mainly on sea mammals such as seals and walruses (but not whales) in addition to caribou (Lester and Shapiro 1968). Therefore, although it appears that during their seasonal occupation of Point Hope, the Ipiutak diet was similar to that of the Tigara, consisting of large quantities of marine fish and seal, the Ipiutak generally substituted caribou for whales (Costa 1980; Costa 1982).

Aleut

Study sample

Aleut dental samples were obtained from the National Museum of Natural History, Washington D.C. These specimens were collected from various of the Aleutian Islands by Hrdlička in 1945. They are mostly protohistoric, dating to after A.D. 1700 (Ungar and Spencer 1999).

Climate

The Aleutian Islands have an arctic tundra vegetation, and a climate very similar to that of Point Hope, Alaska.

Dietary habits

The Aleutian Islanders are known from ethnohistorical reports to have relied almost exclusively on marine animals for their subsistence, including fresh and dried fish,

mollusks, and sea mammals (Hrdlička 1945; Laughlin 1963). Land resources, such as

edible tubers, rodents, and foxes were occasionally eaten as well (Hrdlička 1945;

Laughlin 1963).

Prehistoric/historic hunter-gatherers from Africa

<u>Study sample</u>

The molars included in this study are of hunter-gatherers from South Africa.

These specimens derive from three prehistoric sites (Oakhurst Shelter, Matjes River and

Elands Bay) and one historic site (Riet River). The Oakhurst Rock Shelter lies 13 miles

east of George. It is 2 miles from the lakes that boarder the sea and 4 miles away from the

ocean. Excavations in the site were undertaken in 1932-1935 by AJH Goodwin of the

University of Cape Town. The site is dated to between 9000 and 5000 BP (Morris

1992a). Matjes River Rock Shelter is located on the western side of the mouth of the

Matjes River, east of Robberg. The majority of the skeletal remains from this site were

excavated in the 1920s by Dreyer (Sealy 2006). Additional remains were recovered in the

1950s by Hoffman and Meiring (Sealy 2006). The individuals from Matjes River date to

between 8000 and 2000 BP (Sealy and Pfeiffer 2000). Elands Bay cave lies in the area of

the Cape Deseada at the southern end of the Elands Bay. It is 2 km away from the mouth

of a large freshwater lake (Cowling et al. 1999). The human remains from this site date

from between 11000-9000 and 4000-2000 BP. No human occupation was recorded for

the site between 8000 and 4000 BP. The Riet River skeletons come from the Orange

River Valley, Northern Cape province, and date to between the 11th and 19th centuries AD (Morris 1992b).

Climate

Elands Bay has the mild climatic conditions of a semiarid winter-rainfall coastline of the western fynbos biome (Cowling et al. 1999). The fynbos biome has a Mediterranean climate with mild, wet winters and hot, dry summers. The vegetation is the area is dense shrubland. The terrestrial fauna was dominated by small browsing antelope, and the coastline provided abundant marine life, including shellfish, fish, crustaceans, marine mammals and birds (Parkington 1987). The Oakhurst Shelter and Matjes River sites are in a Montane forest environment (Goodwin 1938). This area is characterized by heavy rainfall in a warm temperate climate. The terrestrial fauna in the area consists mainly of small browsers although some medium sized and large species are also present. Riet River falls in an arid to semi-arid climate characterized by hot summers and cold and frosty winters.

Dietary habits

In these four sites shellfish were found indicating some possibility for fishing activity (Goodwin 1938; Sealy 2006). In Elands Bay, a wide range of marine, estuarine and terrestrial (plants and animal) foods can be harvested close to the site. Carbon-nitrogen isotope analysis of specimens from Oakhurst Shelter, Elands Bay and Matjes River indicate that these individuals had a mixed diet, but included a large amount of marine resources (Sealy 2006; Sealy et al. 1992; Sealy and Pfeiffer 2000; Sealy and van

der Merwe 1986; Sealy and van der Merwe 1988). The Riet River inhabitants had a

mixed subsistence strategy; they were hunter-gatherers and herders (Burchell 1967).

Stable isotopes analysis support this subsistence strategy (Lee Thorp et al. 1993).

Ethographic studies show that 80% or more of the diet of modern Kalahari hunter-

gatherers consists of plant food (Silberbauer 1981).

Chapter 6

Methods

Specimen Preparation

For the purposes of this study, molds of permanent molar tooth crowns of the

fossil and modern human groups were prepared in the American and European

institutions where the specimens are housed. In addition, molds of some of the European

fossils were provided by Alejandro Péréz-Péréz, and molds of some of the Middle

Eastern fossils were provided by Yoel Rak. All molds were prepared following the same

procedure. Specimens were first cleaned with cotton swabs soaked with distilled water.

Acetone and/or ethyl alcohol were used only when the occlusal surface was covered with

a preservative (e.g., Glyptal) that could not be removed with water. Impressions were

then made using Coltene President Jet Regular (polysiloxane vinyl) impression material,

and casts were made with Epo-Tek 501 epoxy resin and hardner (Epoxy Technologies).

This procedure allows for a reproduction of features with a resolution of a fraction of a

micron (Teaford and Oyen 1989a).

Specimen examination

Dental microwear texture analysis, a combination of confocal microscopy and

scale-sensitive fractal analysis, was used in this study for the analysis of dental

microwear. Specimens were examined using a Sensofar Plμ Confocal Imaging Profiler (Solarius Development Inc., Sunnyvale California). Low magnification (10x) was first used to scan the entire occlusal surface and to eliminate teeth that showed obvious postmortem damage and which lacked good microwear preservation. Postmortem damage, which can be caused during either fossilization or collection and preparation of the specimens, is generally easily detected. Naturally caused postmortem wear (e.g., sediment abrasion) will be represented on all surfaces of the tooth and not only the occlusal surface (Grine 1986; King et al. 1999; Teaford 1988), while preparation damage is fairly distinctive (Teaford 1988). Artifact fields caused by glue, dirt, bubbles, etc., stuck to the tooth surface during the molding or casting process are also generally easy to identify with low magnification (Figure 6).

Following Scott et al. (2006; 2005), scans of crushing/grinding facets (i.e., facets 9, 10n, or x) of the specimens with good wear surfaces were taken at a magnification of 100 times with a lateral sampling interval of 0.18 μm and a vertical resolution of 0.005 μm. At this magnification, each scan covers an area of 138 x 102 μm. Four adjoining scans were taken for each surface, resulting in a total area of 276 x 204 μm. Microscopy was conducted at the University of Arkansas at Fayetteville.

Using the Solarmap Universal software (Solarius Development Inc., Sunnyvale, CA), scans were then leveled, modified (to erase defects), and photostimulations and 3D images were generated. This program also allows for the elimination of some identifiable small defects from the analysis, if necessary, either by first tracing their boundaries or by applying the thresholding option and then the erase defect operator in Solarmap. Such

defects can be dust particles, casting bubbles, etc., that are present on an otherwise good surfaces.

The resulting data were analyzed in Toothfrax and SFrax (Surfract, www.surfract.com) using scale sensitive fractal analysis. Scale sensitive fractal analysis follows the principles of fractal geometry, which provide that the appearances of surfaces differ with the scale of observation. In this study, five variables were considered: surface complexity, scale of maximum complexity, anisotropy, heterogeneity, and texture fill volume.

Complexity

Based on the principles of scale sensitive fractal analysis, the area of a rough surface changes with the scale of observation. Thus, at sufficiently coarse scales, surface textures would appear smooth, but these same surfaces would appear rough with increasing resolution at increasingly finer scales (Figure 7). Each surface has a fixed planometric area, which is the two-dimensional area that it occupies. In addition, each surface has a relative area for each scale of observation. Relative areas are calculated by the area-scale tiling algorithm, i.e., by adding all the areas of triangular tiles of a particular scale and dividing this sum by the planometric area of the surface. For each scan, relative areas were calculated for scales ranging from 7200 to 0.02 μm^2. Complexity is characterized by changes in relative area with the scale of measurement. More complex surfaces have microwear features of different sizes overlying each other (Figure 8). The area-scale fractal complexity (*Asfc*) is the slope of the steepest part of the

curve fit to the log-log plot of relative area over the range of scales multiplied by -1000 (Figure 7). *Asfc* was calculated for each scan over one order of magnitude. The *Asfc* values for the four scans were then averaged to provide a mean for each specimen.

Scale of maximum complexity

Scale of maximum complexity (*Smc*) is the scale at which the surface is most complex. It is the fine scale limit of the steepest part of the curve described for the *Asfc* measure. *Smc* values from the four scans for each specimen were averaged to provide a mean *Smc* for each facet.

Anisotropy

Surfaces dominated by many parallel striations tend to be more anisotropic (Figure 9). Each profile has a fixed projected length, but it also has relative lengths for different scales of observation and different orientations (Figure 10). Relative lengths are calculated by the length-scale tiling algorithm, which is the sum of line segments of a given scale fit to a profile divided by the projected length of the same profile. Relative length measures are taken at different orientations for a given scale of observation. These lengths are then defined as vectors and calculated at 5 degree intervals for a total of 36 measurements at each scale. Vectors are then normalized using the exact proportion method by dividing them by the sum of relative lengths from all orientations (Figure 10). This is done to eliminate the effect of pits and scratch depth on the anisotropy graph. The

normalized vectors are displayed graphically in a rosette diagram. The exact proportion Length-scale anisotropy of relief (*epLsar*) is the length of the mean vector at the scale of 1.8 μm. This is the finest scale for which *epLsar* could be determined given the need to balance scale with number of pixels available at all orientations to calculate robust relative length values. Mean *epLsar* values were calculated from the four scans for each specimen.

Heterogeneity

Heterogeneous surfaces will differ in texture from place to place across the surface. Heterogeneity of Area-scale fractal complexity (*HAsfc*) is calculated by dividing the median absolute deviation (the absolute distance between each observation and the median) of *Asfc* by the median *Asfc* for the four scans for each specimen.

Texture fill volume

The volume-filling versus scale algorithm is used to calculate the volume of a surface by filling it with cuboid prisms at different scales (Figure 11). Different scales can be obtained by changing the dimensions of the prisms faces. The distance from the base, where it rests on surface relief, to the highest vertical elevation on the surface forms the rectangular dimension of each cube. With reduction in scale, more cubes fit onto the surface, thus filling a greater volume.

The total volume that is filled changes as a result of variations in two components: the shape of the surface and the texture of the surface. Structural fill volume results from the gross shape of a surface (i.e, it is the fill volume at a sufficiently coarse scale). Texture fill volume, however, is a result of the microwear surface. The textural fill volume was calculated as the total fill volume (generated at a scale of 2 µm) minus the structural fill volume (at a scale of 10 µm). Mean textural fill volume was calculated for each facet from the four scans.

For statistical analyses, a single molar was used to represent each individual. Differences in surface complexity, scale of maximum complexity, anisotropy, heterogeneity and textural fill volume among the modern groups, the Neandertal samples, their predecessors and successors in Europe and their contemporaries in the Levant and between the modern and fossil groups were assessed. All data were rank-trasformed 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, first for the modern groups and then for the fossil groups using multivariate analysis of variance model (MANOVA) (Neff and Marcus 1980). Single classification of variance ANOVAs on each variable along with the multiple comparisons tests were used to determine the sources of significant variation (Sokal and Rohlf 1995). Both Fisher's least significant difference (LSD) and Tukey's honestly significant difference (HSD) post hoc tests were used to balace Type I and Type II errors (Cook and Farewell 1996). Sites that yielded remains of fewer than three individuals were not included in the statistical analyses. However, microwear data of specimens recovered from similar ecogeographic conditions were combined to increase the sample sizes. Finally, the data obtained for the

fossil taxa were compared to those for the modern human samples using the same

parametric statistical scheme used to compare the modern groups and fossil taxa alone.

Chapter 7

Results

Comparative surface scans of the modern and fossil groups are presented in Figures 12 and 13 respectively. Five parameters were considered in this analysis: *Asfc, Smc, epLsar, HAsfc*, and *Tfv*.

Modern samples

The results of the MANOVA statistical tests indicate significant differences among the modern groups considered. Individual ANOVAs show significant differences in all variables except *HAsfc*. Therefore, *HAsfc* will not be considered further here. In the majority of cases, both significant differences among the modern groups are detected by both Fisher's LSD and Tukey's HSD tests.

Comparisons among mainly meat-eating hunter-gatherers

In total, dental samples of five groups of mostly carnivorous hunter-gatherers are included in this analysis. Three of these, the Ipiutak, Tigara, and Aleutians lived in arctic environments whereas two, the Chumash and Fuegians, lived in a Mediterranean climate and an open steppe environment respectively. Differences in the microwear signatures of groups living under similar climatic conditions were first discussed and then differences

in the microwear signatures of the groups that derive from different climatic conditions were examined in an attempt to identify differences that might correspond with their dietary habits.

Groups from similar climatic conditions

This study includes two groups with slightly different dietary habits from Point Hope, Alaska. These two groups are the Ipiutak and Tigara. Fisher's LSD suggests that the Tigara sample has a significantly higher mean *epLsar* value than the Ipiutak (Figure 14; Tables 4-5). No other significant difference was found in the microwear signatures between them. Because of their difference in *epLsar* values, the two Point Hope samples will be treated separately for the purposes of further comparisons.

The three groups of modern hunter-gatherers from arctic climates included in this study are the Ipiutak, Tigara, and Aleutian Islanders. Dental microwear texture analyses reveal significant differences in the signatures of these three groups. Aside from the significant difference in *epLsar* between the two Point Hope populations, the Aleutian Islanders have significantly lower *Asfc* values than those of the two Point Hope groups. Fisher's LSD also suggests that the Aleut have significantly higher *Tfv* than both the Ipiutak and Tigara. No significant difference was found in *Smc* and *epLsar* values between the Aleutian Islanders and the other hunter-gatherer groups from arctic environments (Figure 14; Tables 4-5).

Groups from different climatic conditions

Fisher's LSD suggests that the Fuegians have significantly higher *Smc* and *epLsar* but lower *Asfc* values compared to those of the Chumash (Figure 14; Tables 4-5). Both the Fuegians and Chumash values for *Asfc* are significantly lower than those of the Ipiutak, Tigara, and Aleutians. Compared to the *Smc* values of the three arctic groups, those of the Fuegians are significantly higher (Figure 14; Tables 4-5). The Chumash have *Smc* values that are not significantly different than those of the Aleutians and the two Point Hope groups. The mean *epLsar* value of the Fuegians is significantly higher than that of the Ipiutak, but it does not differ significantly from that of the Tigara and Aleutians. The *epLsar* value of the Chumash does not differ significantly from that of any of the cold adapted modern hunter-gatherers. Significant differences in *Tfv* were found between the Chuamsh and Tigara from the mostly meat-eating modern groups. The Chumash were found to have a significantly higher mean *Tfv* value compared to the Tigara (Figure 14; Tables 4-5).

Comparisons among the mixed diet hunter-gatherers

Molars of mixed diet hunter-gatherers were sampled for African (Khoe-San) Aborigines and individuals who lived in the Andaman Islands. The Khoe-San samples included the prehistoric sites of Matjies River, Elands Bay and Oakhurst Shelter and the historic site of Riet River. The microwear signatures of these for Khoe-San samples were first compared to determine whether they differed in a way that might reflect their dietary habits. Following this, differences and similarities in the microwear signatures among the various mixed diet hunter-gatherer groups were assessed.

The different Khoe-San groups

No significant difference in the microwear signatures of individuals from Matjies River, Riet River, Elands Bay and Oakhurst Shelter were recorded although these samples come from different environments. This is most likely resulting from the high degree of variability of their diets. So these groups were treated as one sample. Therefore, specimens from these four sites were treated as a single sample for the purposes of further comparisons.

Andamanese and Khoe-San

The microwear signature of the Andaman Islanders differs from those of the Khoe-San groups in that the former has significantly higher *Asfc* and lower mean *Smc* (Figure 14; Tables 4-5). No significant differences were found in the *epLsar* and *Tfv* values between these two groups (Figure 14; Tables 4-5).

Mainly meat-eating vs. mixed diet hunter-gatherers

The microwear signature of the Andamanese differs from that of the more carnivorous Fuegians in having significantly higher mean *Asfc* and significantly lower mean *Smc* and *epLsar* values. The Andamanese also differ from the mainly meat eating Aleutians and Chumash in having significantly higher mean *Asfc* and significantly lower mean *Smc*, and they differ from the Ipiutak (detected only by Fisher's LSD) and Tigara (detected by both Fisher's LSD and Tukey's HSD) in having significantly lower mean

Smc and and higher mean *Tfv* (Figure 14; Tables 4-5). The Khoe-San have significantly

higher *Asfc*, but lower *Smc* and, probably, *epLsar* values compared to the Fuegians. They

also have significantly higher *Asfc* values compared to the Chumash. Compared to the

two Point Hope populations, the Khoe-San have a significantly lower *Asfc* and

significantly higher *Tfv* values. No significant differences were recorded between the

microwear signatures of the Khoe-San and the Aleutian Islanders (Figure 14; Tables 4-5).

Fossil samples

The results of the MANOVA statistical tests indicate significant differences

among the fossil groups considered. Individual ANOVAs show significant differences in

Asfc only.

Temporal and geographical comparisons within the Neandertal sample

The Neandertal specimens included in this study were recovered from different

ecogeographic conditions. To understand the effects of climatic and vegetation changes

on their dietary habits, the microwear signatures of specimens from the same

geographical area but dating to different oxygen isotope stages were compared. In

addition, the microwear signatures of specimens dating to the same oxygen isotope stage

but recovered from different geographical regions were compared. Comparisons between

specimens from different geographic areas and different OIS wherein the environmental

reconstructions indicate similar environments were not possible from the present dataset.

Northern Europe: Only one specimen from northern Europe, Spy 1 fossil, was included in this analysis, therefore, statistical comparisons are not possible for this area.

Central Europe: The Neandertal fossils analyzed from central Europe date to OIS 3 (sites of Vindija, St. Césaire, and La Quina) and OIS 4 (site of Subalyuk). Climatic reconstructions suggest that the specimens from OIS 3 were deposited at a time when the vegetation was coniferous forest, whereas the specimen from OIS 4 was deposited in a steppe environment. Since there is only one specimen dating to OIS 4, statistical comparisons between these two samples are not possible. It should be noted, however, that Subalyuk 1 has an *Asfc* value that is lower than those of all the OIS 3 fossils (Figures 15-16). Also, its *Smc* value is higher than those of all the OIS 3 specimens except Vindija 11.46 (Figures 15-16; Tables 7-8). The Subalyuk 1 value for *epLsar* falls within the range established by the OIS 3 specimens (Figures 15-16).

Southern Europe: The Neandertal specimens from southern Europe can be divided into three groups: those dated to OIS 3 (Sidron 1 and 2, and Zafarraya), one dated to OIS 4 (Guattari 3) and two dated to OIS 5e (Saccopastore 1 and 2). The three Neandertals from OIS 3 lived in a deciduous forest environment, those from OIS 4 lived in a steppe environment, whereas those from OIS 5e were deposited at a time when the vegetation of the area was a Mediterranean forest. The small sample sizes preclude statistical comparisons among these three groups. However, among these specimens, Guattari 3 has the lowest *Asfc* value. The two Saccopastore specimens have *Asfc* values that are

higher than that of Guattari 3, but they all fall outside the observed range for specimens from OIS 3 (Figures 15-16).

The *Smc* values of the southern European Neandertals do not show clear and consistent differences according to the various oxygen isotope stages. Nevertheless, it is worthwhile to note that Sidron 1 and Saccopastore 2 have *Smc* values that are very high compared to the rest of the specimens from southern Europe (Figures 15-16). The Saccopastore 1 *Smc* value falls within the range of *Smc* values of the specimens dating to OIS 3. Guattari 3 has a value higher than those of all the specimens from the three groups except Saccopastore 1 and Sidron 1. The values for *epLsar* do not show any differences that correspond to the oxygen isotope stages from which the molars derive (Figures 15-16).

Levant: Statistical comparisons are not possible for the specimens from the Levant since the sample sizes from the different oxygen isotope stages are low. Nevertheless, Amud 1 has the highest *Asfc* value followed by Tabun 1, Kebara 2 and Tabun 2 in decreasing order. *Smc* values for these specimens decrease in order as followes: Tabun 2, Tabun 1, Kebara 2 and Amud 1. Tabun 1 has the highest *EpLsar* value followed by Kebara 2, Tabun 2 and Amud 1 (Figures 15-16).

Same OIS but different geographical area

OIS 3: Neandertal specimens dating to OIS 3 are available from northern, central and southern Europe as well as the Levant. The Spy Neandertal from northern Europe inhabited an area covered by shrub tundra vegetation. Specimens from central and southern Europe existed in forested environments and those from central Europe lived in

coniferous forests. The Neandertals in southern Europe lived in a deciduous forest. Only one Levantine specimen, Amud 1, dates to OIS 3 and one, Kebara 2, dates to the transitional period between OIS 4 and OIS 3. Amud 1 lived in a mix of coniferous and deciduous forest vegetation, whereas Kebara 2 lived in a mix of woodland and semi-desert environments. With regard to dental microwear texture, the Neandertals from central Europe have significantly lower *Asfc* values than those from southern Europe (Figures 15-16; Tables 6-7). The *Asfc* value for Spy 1 is lower than those of specimens from southern Europe, but it falls within the range of those from central Europe. Its values for *Smc* and *epLsar* fall within the ranges of both groups (Figures 15-16). Amud 1 has a relatively high *Asfc* value, falling within the range of values for specimens from southern Europe (Figures 15-16). Its *Smc* values fall within the ranges of the other European Neandertals. The *epLsar* value of Amud 1, however, is among the lowest of all the fossil specimens examined (Figures 15-16). Kebara 2 has *Asfc*, *Smc*, and *epLsar* values that fall within the observed ranges of central European Neandertals (Figures 15-16).

OIS 4: Two Neandertal specimens (Guattari 3 and Subalyuk 1) date to OIS 4. Both of these individuals lived in a steppic environment. Their *Asfc* values are very similar to one another, but Subalyuk 1 has an *Smc* value which is slightly higher than that of Guattari 3 (Figures 15-16). Both specimens have *ASFC* values that are lower than those of the OIS 3 specimens (Figures 15-16).

OIS 5: Only two specimens from one site (Saccopastore) date to OIS 5e. Thus, no comparisons between specimens from different regions are possible for this oxygen isotope stage (Figures 15-16).

OIS 6: Only the site of Tabun dates to OIS 6. Thus, no comparisons between specimens from different regions are possible for this oxygen isotope stage (Figures 15-16).

Difference within the Pre-Neandertals

The European Pre-Neandertals also lived in the changing environments of the Ice Age. Paleoenvironmental reconstructions indicate that the Arago, Montamurin and Mauer individuals inhabited steppe environments, whereas those from Atapuerca-Sima de los Huesos, Steinheim and Pontnewydd came from a wooded environment. The Pre-Neandertals from steppe environments have *Asfc* values that are significantly lower than those from wooded environments (Figures 15-16; Tables 7-8).

Comparisons between the Pre-Neandertals and the Neandertals

Possible differences in the dietary habits of the Neandertals and Pre-Neandertals were assessed through the comparisons of the microwear signatures of specimens that derive from similar as well as different climatic conditions.

Pre-Neandertals vs. Neandertals from wooded environments (OIS 3 and OIS 5e)

Neandertals from wooded environments are known from central Europe and the Levant during OIS 3 and from southern Europe during both OIS 3 and OIS 5e. No

siginificant differences between the Pre-Neandertals and Neandertal groups from wooded environments were found (Figures 15-16; Tables 7-8).

Only two specimens, Saccopastore 1 and 2, are known from southern Europe that date to OIS 5e and one specimen, Amud 1, from the Levant that dates to OIS 3. The small sample sizes of these two Neandertal groups do not allow for statistical comparisons with the Pre-Neandertals. It should be noted though that the *Asfc* values for the two Saccopastore specimens fall within the range of *Asfc* values for the Pre-Neandertals recovered from the woodland deposits (Figures 15-16). Saccopastore 2 has the second highest *Smc* value among all the fossil specimens examined in this study including this Pre-Neandertal group, whereas the *Smc* value of Saccopastore 1 falls within the range of variation of the Pre-Neandertals living in wooded environments (Figures 15-16). The opposite pattern is seen for the *epLsar* values of the Saccopastore specimens. The *Asfc* value of the Amud 1 specimen is slightly higher than that of the Pre-Neandertals from wooded deposits (Figures 15-16). The Amud 1 *Smc* value falls within the range of the Pre-Neandertal group. Amud 1 has very low *epLsar* value which is lower than the values for most of the fossil specimens examined.

Pre-Neandertals from steppe environments vs. Neandertals from wooded environments

There are significant differences in the microwear signatures of the Pre-Neandertals that lived in steppe conditions and the Neandertals from the wooded environments of central and southern Europe. The *Asfc* value of the Pre-Neandertals is significantly lower than that of the Neandertals (Figures 15-16; Tables 7-8). One of two specimens from southern Europe OIS 5e (Saccopastore 2) and Amud 1 have *Asfc* values

that exceed the range of values for the Pre-Neandertals from steppe environments (Figures 15-16). Saccopastore 1 has an *Asfc* value that falls within the range of variation of the Pre-Neandertal group (Figures 15-16). *Smc* and *epLsar* values for the two Saccopastore specimens and the Amud 1 Neandertal fall outside the range of variation of the Pre-Neandertals from steppe environments (Figures 15-16).

<u>Pre-Neandertals from wooded and steppe environments vs. Neandertals from steppe environments</u>

Statistical comparisons are not possible for this category since there are only two Neandertal specimens recovered from steppe environments. These two specimens, Subalyuk 1 and Guattari 3, have *Asfc* values that are lower than those of the Pre-Neandertals from wooded environments, but they fall within the observed range for Pre-Neandertals from steppe environments (Figures 15-16). As with the *Smc* values of Subalyuk 1 and Guattari 3, they fall within the range of both Pre-Neandertal groups, but it should be noted that the Arago 13 specimen considerably extends the range of *Smc* values of the Arago sample (Figures 15-16). Arago 13 has a very low *Smc* value; it is lower than those of Subalyuk 1 and Guattari 3. *EpLsar* value of Subalyuk 1 falls within the range of both Pre-Neanderal groups (Figures 15-16). The Guattari 3 Neandertal has an *Smc* value that exceeds the range for Pre-Neandertals from wooded environments, but it falls within the range of those from steppe environments (Figures 15-16).

Difference within the early Upper Paleolithic sample

The sample from the Upper Paleolithic sites is very small and does not permit statistical comparisons among specimens from different regions. However, it should be noted that values for all three variables for specimens from southern Europe range rather widely, and within the ranges of variation of these variables for specimens from central Europe (Figures 15-16). Since there appears to be considerable overlap between microwear patterns of specimens from southern and central Europe, the early Upper Paleolithic will be grouped together for the purposes of comparisons with the other fossil and modern groups.

Comparisons between early Upper Paleolithic sample and Neandertals

Comparisons between the early Upper Paleolithic (EUP) specimens and the Neandertal groups that date to OIS 3 from southern and central Europe reveal significant differences between the EUP and the Neandertals from southern Europe, but not from central Europe. The southern European OIS 3 Neandertals have significantly higher *Asfc* values compared to the EUP group (Figures 15-16; Tables 7-8). Although statistical comparisons are not possible for the rest of the Neandertals, it should be noted that the *Asfc*, *Smc* and *epLsar* values for these Neandertals fall within the ranges of variation established by the EUP specimens (Figures 15-16).

Comparisons between early Upper Paleolithic humans and Pre-Neandertals

No significant difference was found between the microwear signatures of the early Upper Paleolithic specimens and either of the Pre-Neandertal groups (Figures 15-16; Tables 7-8).

Comparisons between early anatomically modern humans and other fossil groups

Unfortunately, microwear was successfully recovered from only one specimen, Skhul 7, considered to be an early anatomically modern human. Therefore, no statistical comparison between the microwear variables of this specimen and the other fossil groups was possible. However, it should be mentioned that this specimen has an *Asfc* value that falls within the range of variation of the Neandertals from southern Europe that date to OIS 3; its *Asfc* value is higher than those for all other Neandertals except Amud 1 and Tabun 1. The Skhul 7 *Smc* value is higher than most of the values of the Neandertal specimens examined except La Quina 5, Vindija 11.46, Sidron 1 and Saccopastore 2. Its *epLsar* value is relatively low, and falls within the range of variation of the Neandertals from central Europe dating to OIS 3 (Figures 15-16). Compared to the Pre-Neandertals, the *Asfc* and *epLsar* values of Skhul 7 fall within the ranges of variation of the two Pre-Neandertal groups, and its *Smc* value falls within the range of the Pre-Neandertals from steppe environment (Figures 15-16). The Skhul 7 values of *Asfc*, *Smc*, and *epLsar* fall within the ranges established by the early UP sample (Figures 15-16).

Comparisons between the fossil and modern groups

The results of the MANOVA statistical tests indicate significant differences between the fossil and the modern groups considered. Individual ANOVAs show significant differences in *Asfc, Smc* and *epLsar*.

Comparisons between Neandertals and recent groups

The Neandertals from central Europe that date to OIS 3 and who inhabited forested environments have a significantly lower mean *Asfc* value than all the modern groups except the Chumash and Fuegians (Figure 17; Table 8). Fisher's LSD suggests that this fossil group differs from the Fuegians in having a higher mean *Asfc*. There is no significant difference in mean *Asfc* between this fossil group and the Chumash (Figure 17; Table 8). Mean *Smc* of the OIS 3 central Europe Neandertals is significantly higher than the Andamanese, Ipiutak, Tigara and Aleut averages, but is not significantly different from those of the San, Chumash, and Fuegians (Figure 17; Table 8). Fisher's LSD results hinted that this Neandertal group has lower *epLsar* than the Fuegians (Figure 17; Table 8). The dental microwear texture analysis indicates that the dietary habits of the OIS 3 Neandertals from central Europe had a diet similar most similar to those of the Chumash the modern groups analyzed.

The microwear signature of the OIS 3 Neandertals from southern Europe who inhabited wooded environments differs from that of the Fuegians in having a significantly higher mean *Asfc*. Fisher's LSD also suggests that the southern European OIS 3 Neandertals have higher mean *Smc* compared to the Andaman Islanders, Ipuitak, Tigara, and Aleut and higher *Asfc* compared to the Chumash (Figure 17; Table 8). There is no

significant difference in *epLsar* between this group of Neandertals and any of the modern

hunter-gatherers examined (Figure 17; Table 8). These results suggest that this group of

Neandertals from southern Europe had varied diets.

The only specimen dating to OIS 3 from northern Europe (Spy 1) has an *Asfc*

value that falls within the ranges of the Tigara, and Chumash, but outside the ranges of

variation of the rest of the modern human groups (Figure 17). The *Smc* value of the Spy

specimen falls within the ranges of variation of the Andamanese, Tigara, Khoe-San,

Aleut and Chumash (Figure 17). The Spy specimen's *epLsar* value falls within the ranges

of variation of all the modern human groups (Figure 17).

Statistical comparisons between the OIS 4 Neandertals from central and southern

Europe and the modern groups could not be conducted since there is only one specimen

dating to this period from central Europe and one from southern Europe. These two

individuals, however, have low *Asfc* values, which place them within the lower part of

the Fuegian range and below the ranges of all other recent human groups (Figure 17). The

Smc value of Subalyuk 1 (central Europe) exceeds one standard deviation of the mean of

any modern group (Figure 17). The *Smc* value of Guattari 3 (southern Europe) falls

within the observed ranges of the Tigara, Aleut, Chumash and Fuegian samples (Figure

17). The *epLsar* values for these two Neandertal specimens fall within the ranges of all

modern human hunter-gatherers (Figure 17). Since *Asfc* appears to be the most diagnostic

variable with regard to detecting differences between the modern groups, this may

suggest that the diets of the OIS 4 Neandertals were most similar to those of the

Fuegians.

The OIS 5e Neandertal specimens from southern Europe could not be statistically compared to the modern hunter-gatherer groups because only two (Saccopastore 1 and 2) represent this group. The *Asfc* values of both fall within the ranges of the Chumash and Tigara, but higher than the range of Fuegians and lower than the ranges of all other modern human groups (Figure 17). The *Smc* values of the Saccopastore specimens are very different from one another. The Saccopastore 1 *Smc* value falls within the ranges of all modern groups, whereas the Saccopastore 2 value is much higher than the value of any modern group (Figure 17). The *epLsar* value of Saccopastore 1 is relatively high, and falls within the range only of the Fuegians; and that of Saccopastore 2 falls within the ranges of most modern hunter-gatherer groups (Figure 17).

Four Neandertal specimens from the Levant are considered here: Tabun 1 and 2, Kebara 2 and Amud 1. The *Asfc* and *Smc* values for Tabun 1 fall within the ranges of most of the modern human groups, except Fuegians and Chumash (Figure 17). Its *epLsar* value falls within the ranges of all modern groups except the Chumash (Figure 17). The Tabun 2 *Asfc* value falls within the ranges of only the Fuegians and Chumash, whereas its *Smc* value falls within the ranges of most of the modern human groups except the Ipiutak and Fuegians (Figure 17). The *epLsar* value of Tabun 2 falls within the range of all modern hunter-gatherers except the Fuegians (Figure 17). The *Asfc* value of the Kebara 2 Neandertal places it within the ranges of Chumash, Khoe-San, Aleut and Tigara (Figure 17). The Kebara 2 *epLsar* value falls within the ranges of all modern groups except the Fuegians. The *Asfc* value of the Amud specimen falls within the range of all modern groups except the Chumash and Fuegians (Figure 17). The *Smc* values for both Kebara 2 and Amud 1 fall higher than the range of the Ipuitak and lower than the range of the

Fuegians, but within the ranges of all other modern hunter-gatherer samples (Figure 17).

Finally, the *epLsar* value of Amud 1 falls within the range of variation of only the

Ipiutak, and is lower than the ranges of all remaining modern groups (Figure 17).

Comparisons between the Pre-Neandertals and recent groups

The group of Pre-Neandertals from wooded environments (n=10) has

significantly lower mean *Asfc* value than the Ipiutak, Tigara, Andamanese, and Khoe-San

(Figure 17; Table 8). This Pre-Neandertal group also has significantly higher mean *Smc*

compared to the Andamanese and Khoe-San. Fisher's LSD also suggests that the

microwear signature of this Pre-Neandertal group differs from those of the Aleut, Ipiutak

and Tigara through its higher mean *Smc*, and from that of the Fuegians through its higher

mean *Asfc* value (Figure 17; Table 8). The microwear pattern of this Pre-Neandertal

group is indistinguishable from that of the Chumash (Figure 17; Table 8). No difference

in anisotropy was found between the Pre-Neandertals and any of the modern human

groups except the Fuegians, with the latter probably having significantly more anisotropic

microwear features (Figure 17; Table 8). Overall, the results suggest that the Pre-

Neandertals from wooded environments had microwear fabrics most similar to those of

the Chumash.

The group of Pre-Neandertals from steppe environments (n=5) has significantly

lower mean *Asfc* values than all of the modern groups except the Fuegians and

significantly higher mean *Smc* than the Ipiutak, Andamanese and Khoe-San (Figure 17;

Table 8). Fisher's LSD results also indicate that this Pre-Neandertal group has

significantly higher mean *Smc* than the Tigara, Aleut, and the Chumash. Significantly

higher *epLsar* values are also indicated by Fisher's LSD results which differentiate this

group of Pre-Neandertals from the Ipiutak, Andamanese, Khoe-San, and Chumash

(Figure 17; Table 8). No significant difference was found in any of the variables between

the Fuegians and this Pre-Neandertal group suggesting that these fossils had wear fabrics

most similar to those of the Fuegians among the modern groups (Figure 17; Table 8).

Comparisons between early Upper Paleolithic and recent groups

The early Upper Paleolithic sample that derives from wooded environments

(n=15) has significantly lower mean *Asfc* values compared all of the modern human

groups except the Chumash and Fuegians (Figure 17; Table 8). The early Upper

Paleolithic sample also differs from the Andamanese and Khoe-San in having

significantly higher mean *Smc* value compared to these modern groups. It might also

have significantly higher *Smc* value compared to the Ipiutak, Tigara, and Aleut according

to the Fisher's LSD results. No significant difference was found either in *Smc* or *Asfc*

between the early UP sample and the Fuegians and Chumash (Figure 17; Table 8). The

only difference between the microwear signatures of the EUP and Fuegian sample is

hinted by the Fisher's LSD results in the mean *epLsar* value, which is higher in the latter

(Figure 17; Table 8). These data indicate that the EUP humans from wooded

environments had somewhat varied diets, although it also suggests that their diets were

mostly similar to those of Chumash and the Fuegians from the modern samples.

Comparisons between anatomically modern humans and the recent groups

The Skhul 7 *Asfc* value falls within the ranges of the Chumash, Khoe-San, Aluetian Islanders and Tigara, and outside the range of the other recent hunter-gatherer groups (Figure 17). The *Smc* value of Skhul 7 is higher than those of all recent groups considered (Figure 17). Its *epLsar* value falls within the observed ranges of all the modern groups except the Fuegians, Aluetian Islanders and Tigara (Figure 17). The microwear data place Skhul 7 within ranges of modern groups with different dietary habits probably suggesting a somewhat varied diet for this individual.

Summary of the comparisons between the fossil and recent groups

To summarize the results of the comparisons between the fossils and the recent groups in an efficient manner and to include the isolated Neandertal specimens, Figure 18, represents the results of a hierarchical cluster analysis using Euclidean distance and complete linkage. This cluster is for the complexity variable since it best illustrates the results of the post-hoc tests.

The Andaman, Tigara, and Ipiutak modern groups have the highest surface complexity most likely as a result of their food preparation techniques which allowed for the the ingestion of grit particles attached to their diets. This will be discussed in more detail in the following chapter. The thing to note is that none of the fossil specimens and groups cluster close to these modern samples suggesting that the ingestion of non-dietary grit particles does not cause a problem in the differentiation of the fossil groups. The

second cluster includes the Neandertals from southern Europe OIS 3 from deciduous forests in addition to the Amud and Tabun 1 specimens. These cluster with the Khoe-San mixed diet hunter-gatherers. The Pre-Neandertals and Neandertals from steppe environments in addition to Tabun 2 cluster closest to the Fuegians from the modern groups. Finally, the pre-Neandertals from wooded environments, the Neandertals from the coniferous forests of Central Europe OIS 3, Saccopastore, spy, Kebara, the anatomically modern human from skhul and the early upper Paleolithic specimens, all cluster in close proximity to the Chumash.

Chapter 8

Discussion

Modern sample

With the exception of the studies by Hojo (2001), Molleson et al. (1993), Pastor (1992), and Teaford (1991), occlusal microwear of pre-agricultural modern human groups has not been documented. In this study, the occlusal microwear signatures of seven modern hunter-gatherer groups with varied dietary habits were examined in order to establish whether differences in their diets are reflected on the occlusal surfaces of their molars, and to provide a comparative database for the interpretation of fossil hominin wear patterns. Previously, the occlusal microwear signatures of fossil hominins have been compared only to those of living non-human primates. However, modern humans have dietary habits very different from those of non-human primates. The diets of modern humans may be more varied and, in particular, their meat intake is generally much greater. The Neandertals lived a hunter-gatherer way of life. Thus, comparing their microwear signature to those of historic and prehistoric hunter-gatherers, especially those living under similar climatic conditions, rather than non-human primates, should lead to a better understanding of their subsistence patterns.

The seven modern hunter-gatherer groups included in this study come from different geographical regions and live under a variety of climatic conditions, ranging from arctic to tropical environs. Based on their dietary habits, these groups can be divided

into two major categories: 1) mainly meat eaters (Ipiutak, Tigara, Aleutian Islanders, Chumash and Fuegians), and 2) mixed diet hunter-gatherers (Khoe-San and Andamanese). The group that consumed mostly meat can be further divided into three categories based on habitat: 1) those from arctic environments (Ipiutak, Tigara, and Aleutian Islanders), 2) those from cold-steppe environments (Fuegians), and 3) those from Mediterranean climate (Chumash). Differences in the dietary habits of the modern groups were clearly reflected in their dental microwear patterns. Significant microwear differences between the principally carnivorous and the mixed diet hunter-gatherers were detected, and finer scale divisions within each of these dietary categories were also observed. Subtle differences between the microwear signatures of the two Point Hope populations were also detected.

Based on complexity of the surface texture, the modern samples can be divided into four groups in decreasing order of complexity: 1) Tigara, Andamanese, and Ipiutak, 2) Aleutian Islanders and Khoe-San, 3) Chumash, and 4) Fuegians (Figure 19). With only two exceptions, the Aleutian Islanders and the Andamanese, this division reflects both the dietary habits and the geographical locations of these groups (Figure 19). The scale of maximum complexity differentiates the Fuegians and the Andamanese from the other modern human samples. The Fuegians have the highest *Smc* value, whereas the Andamanese have the lowest (Figure 19). The remaining groups (i.e., Aleutian Islanders, Ipiutak, Tigara, Chumash and Khoe-San) occupy an intermediate position with respect to this variable. The results of this study indicate that the Fuegians exhibit the most anisotropic surfaces of all the modern groups except the Tigara, and the Tigara also have significantly more anisotropic surfaces than the Ipiutak. Texture fill volume differentiates

the two Point Hope populations, as having the lowest values, from the Aleutian Islanders, the Andamanese and Khoe-San. Heterogeneity of surface texture does not differentiate between the modern groups.

The two mostly carnivorous hunter-gatherer groups from the arctic environments of Point Hope, the Ipuitak and Tigara, cluster together and have the most complex surfaces among the groups analyzed (Figure 19). The high levels of surface complexity might be linked to a highly abrasive diet. Archaeological and ethnological accounts indicate that the diet of the two Point Hope populations was similar, consisting of large quantities of meat (Larsen and Rainey 1948; Lester and Shapiro 1968). The archaeological evidence, however, indicates that the Tigara had a mainly marine diet relying on whale meat, fish and seal, whereas the Ipiutak were mainly caribou hunters, although they included high amounts of fish and seal during their seasonal occupation of the coast (Larsen and Rainey 1948; Lester and Shapiro 1968). Ethnological evidence suggests that the two Point Hope groups dried their meat on open racks or kept it frozen underground as a year long staple (De Poncins 1978; Giddings 1967). Point Hope has numerous sandy beaches, and freezing meat on open racks or its underground storage would have provided ample opportunity for sand to be integrated in it. Thus, the food preparation techniques of the two Point Hope populations probably lead to high incidences of extraneous abrasive particles being ingested. Microwear texture analysis detects differences in anisotropy between these two Point Hope groups. The Tigara have significantly more anisotropic surfaces than the Ipiutak. Archaeological evidence suggests that the Tigara relied on whaling, whereas the Ipiutak did not include this in their diet (Larsen and Rainey 1948; Lester and Shapiro 1968). The difference in

microwear signature might correspond to dietary differences, but this correlation cannot

be confirmed. Stable isotope analyses have not yet been conducted on these remains.

Since this technique can distinguish between marine and terrestrial diets (e.g., Keegan

and DeNiro 1988; Schoeninger and DeNiro 1984), it can be used to test whether the

Ipiutak had a predominantly terrestrial (caribou) diet with seasonal dependence on marine

resources, and whether the Tigara had a predominantly marine diet.

Although the Aleutian Islanders lived in arctic/tundra environment similar to that

of Point Hope, they have a level of surface complexity that is significantly lower than

both the Ipiutak and Tigara (Figure 19). The Aleutian Islanders cluster with the mixed

diet Khoe-San (Figure 19). Ethnohistorical reports indicate that the Aleuts, like the two

Point Hope populations, relied almost exclusively on meat for their subsistence (Hrdlička

1945; Laughlin 1963). Their diet consisted of fresh and dried fish, mollusks, and sea

mammals (Hrdlička 1945; Laughlin 1963). The significant differences in complexity

between the Aleutian Islanders and the Tigara and Ipuitak might reflect differences in the

amount of extraneous abrasive particles being ingested, rather than diet. Unlike Point

Hope, Alaska, the Aleutian Islands consist of volcanic landscapes that lack sandy

beaches. This would have reduced the amount of attachment of grit or sand particles to

the food as a result of food preparation techniques (such as drying meat), thus resulting in

less complex surfaces in the Aleutian teeth compared to the two Point Hope populations.

Occlusal molar microwear data using the SEM with the semi-automated method

following Ungar (1995) have been previously collected from the same Ipiutak, Tigara

and Aleut specimens included in this study (El Zaatari 2006). This allows for the

comparison of the results attained using two different methodologies (SEM and

MICROWARE and microwear texture analysis). The results of the SEM analysis (Table 9-10) show that the microwear fabrics of the two Point Hope populations have significantly higher numbers of features and narrower scratches compared to the Aleutian Islanders (El Zaatari 2006). The Tigara were also found to have significantly higher incidence of pitting compared to the Aleut (Table 9-10). These results also support the notion that the two Point Hope populations had a more abrasive diet compared to the Aleuts and show that microwear data collected using different techniques give analogous results.

Concerning the two mostly carnivorous hunter-gatherer samples from warm climates, the Chumash and Fuegians have the lowest surface complexity among the groups considered, including the mostly meat eaters from the arctic, thus indicating a relatively low abrasive diet for both the Chumash and Fuegians (Figure 19). The Chumash were fishers and hunters whose diet was based on fish, marine mammals and other marine resources (e.g., shellfish) (Fagan 1995). They also hunted small terrestrial animals available on the island (Fagan 1995). The Fuegians relied on fishing and seal-hunting, although seals rank lower in importance (Bridges 1885; Snow 1861). Guanaco (*Lama guanicoe*) might have also formed a terrestrial source of food for the Fuegians (Yesner et al. 2003). Unlike the inhabitants of Point Hope and the Aleutian Islands, the Chumash and Fuegians did not dry their meat or store it underground. Thus, the low levels of surface complexity for the Chumash and Fuegians reflect a diet low in abrasives. This is consistent with a highly carnivorous diet with low amounts of extraneous abrasive particles ingested as a result of food preparation techniques.

The differences between the microwear signatures of the Chumash and Fuegians probably suggest slight differences in the diets of these two groups (Figure 19). The significantly higher surface complexity and lower scale of maximum complexity levels of the Chumash compared to those of the Fuegians (Figure 19), suggest that the Chumash ingested more abrasive particles that were relatively smaller than those ingested by the Fuegians. Ethnohistoric accounts indicate that although both groups relied on marine animals and some terrestrial ones for food, the Chumash also relied on several kinds of plants including islay, manzanite, mangle berries, tarweed seeds, tubers and sage (Timbrook 1993; Walker 1996). The differences in the microwear signature of these two groups might be linked to the Chumash's inclusion of such plants in their diet. However, this remains a suggestion as there is no mention in the ethnohistoric records whether the Fuegians included any plants in their diets. These records only mention that the Fuegians, especially the Yamana tribe, to which specimens included in this study belong, relied almost exclusively on marine animals for their subsistence (Bridges 1885; Snow 1861).

The carbon-nitrogen signatures of Fuegians and Chumash suggest that these two groups relied mainly on marine animals for their subsistence (Walker and DeNiro 1986; Yesner et al. 2003). The low levels of occlusal microwear surface complexity of these groups reflect this mainly carnivorous diet, which did not include a large amount of abrasive particles. Thus, the stable isotopes and microwear data are in agreement here. Unfortunately in this case, since ethnographic accounts state that the Fuegians diet consisted of large amounts of shellfish (Bridges 1885; Snow 1861), the stable isotope signature cannot clarify whether the Chumash included slightly more terrestrial resources in their diet compared to the Fuegians, since a marine diet with high amounts of low

trophic-level food (such as shellfish) gives a very similar carbon-nitrogen signature to a one which is predominantly based on marine foods, but included some terrestrial resources (Katzenberg and Weber 1999; Schoeninger et al. 1983).

The Khoe-San mixed diet hunter-gatherers exhibit levels of surface complexity significantly lower than those of the meat eaters from Point Hope and significantly higher than those of the meat eaters from warmer climates (Figure 19). The Khoe-San had a diet consisting of a wide range of marine, estuarine and terrestrial (plants and animal) foods (Burchell 1967; Goodwin 1938; Sealy 2006). Ethographic studies show that 80% or more of the diet of modern Kalahari hunter-gatherers consists of plant food (Silberbauer 1981). Even though the Kalahari is quite sandy, it should be mentioned that the San do not dry meat or store it underground. It is reasonable to suggest that the abrasives ingested by the Khoe-San are not due to dust or sand particles attached to their dietary staples, but rather due to the ingestion of hard dietary items such as nuts, seeds, tubers, etc, that are widely available and exploited by these hunter-gatherers.

The Khoe-San sample included in this study is comprised of specimens from the sites of Oakhurst Shelter, Elands Bay, Matjes River and Riet River. The results of stable isotope analyses indicate that the diets of the inhabitants of these four sites were similar (Burchell 1967; Sealy 2006; Sealy et al. 1992; Sealy and Pfeiffer 2000; Sealy and van der Merwe 1986; Sealy and van der Merwe 1988). The carbon and nitrogen signatures of these groups show that they all had a mixed diet consisting both of marine and terrestrial (plant and animal) resources (Burchell 1967; Sealy 2006; Sealy et al. 1992; Sealy and Pfeiffer 2000; Sealy and van der Merwe 1986; Sealy and van der Merwe 1988). In accordance with the stable isotopes results, microwear texture analysis did not detect any

significant differences in the occlusal microwear signatures of these four Khoe-San groups. Also, the dental microwear results are in agreement with the stable isotope data in classifying the Khoe-San as having a mixed diet.

The Andaman Islanders have relatively complex surfaces, which place them with the Point Hope populations (Figure 19). Also, the surfaces of the Andamanese attain maximum complexity at relatively fine scales indicating the presence of numerous small microwear features that overly one another. Although the mixed-diet Andamanese come from a tropical environment, historic accounts indicate that these people relied more on hunting and fishing than gathering plants for their subsistence (Myka 1993). Unlike the Khoe-San, whose diet consisted more of plants than meat, meat comprises some 66% of the Andamanese diet (Man 1883). However, this does not explain why the Andamanese have such complex surfaces placing them with arctic hunter-gatherers rather than with carnivorous hunter-gatherers from warmer climates, such as the Chumash and the Fuegians. Historic accounts also note that the Anadamanese diet consisted mostly of meat that was eaten half roasted, such that it remained relatively tough (Pal 1984). The food was usually cooked uncovered, which would have enabled contamination by windborne sand (Man 1883; Pal 1984). The high complexity of the surfaces of the Andamanese molars might thus reflect their food preparation techniques which allowed for very small abrasive particles to be attached and ingested with their food.

Buccal microwear of individuals belonging to several modern groups were analyzed by Lalueza et al. (1996). Although differences in buccal microwear were detected, namely that carnivorous hunter-gatherers were found to have fewer striations and higher proportion of vertical striations compared to those with mixed diet (Lalueza et

al. 1996), these results cannot be considered very reliable due to sampling problems. Included in the Lalueza et al. (1996) study of buccal microwear are dental samples belonging to mainly modern carnivorous hunter-gatherers (Fuegians, Inuit, Lapps, and Vancouver Islanders), mixed diet hunter-gatherers (Bushmen, Tasmanians, Australian Aborigines, Andamanese and Veddahs) and agriculturalists (Hindu groups of Bihar and Orissa region). Although the authors tried to select human groups with a characteristic biological and ethnological identity, they mention that some groups were highly heterogeneous (Lalueza et al. 1996). Indeed, information on tribal attribution, exact location of recovery and date of many of the specimens included in that study, especially those housed at the British Museum of Natural History, are lacking. Such information is essential for classifying groups based on dietary and environmental factors. For example, Lalueza et al. (1996) mention that their sample of Fuegians consists of individuals from three groups: the Selknam, Kawesker, and Yamana. Ethnohisotric and archaeological accounts show that the dietary habits of these three groups were significantly different (e.g., Bridges 1885; Snow 1861; Yesner et al. 2003). For example, the Yamana, were maritime hunter-gatherers living in the Beagle Channel and the islands to the south, whereas the Selknam were terrestrial hunter-gatherers occupying southernmost Patagonia (Bridges 1885; Snow 1861; Yesner et al. 2003). Lalueza et al. (1996) assume that groups that are closely related are likely to have similar diets. However, as seen from the Fuegians example, ethnohistoric and archaeological records clearly refute this assumption. Also, the diets of these hunter-gatherer groups changed through time, especially before and after contact with Europeans (e.g., Yesner et al., 2003). Thus, knowing the date for the included specimens is essential before attempting an analysis of

the correlation of buccal microwear and the dietary habits of these groups. The samples of Australian aborigines, Bushmen, Inuit, and Vancouver Islanders used by Lalueza et al. (1996) all face such problems. Therefore, these samples cannot be considered appropriate for their study that was aimed at understanding the causative factors behind the buccal microwear pattern of modern humans. These samples are thus certainly unsuitable to be used as a comparative database for the fossil specimens (i.e., Pre-Neandertal, Neandertals, Upper Paleolithic humans) that they and Pérez-Pérez et al. (2003) examined. Thus, such sampling problems might have lead Pérez-Pérez et al. (2003) to state that "there seems to be a mismatch between the buccal microwear patterns of the fossil samples studied and those of the comparative modern human populations," and then conclude that "modern models of microwear might not be representative of past populations' diet." For the current study of occlusal microwear analysis, modern samples were carefully selected such that adequate information on their attribution, location, date and dietary habits is available.

The results of the occlusal molar microwear analysis show that dental microwear texture analysis is able to differentiate between modern humans with different dietary habits. Five variables were gleaned from occlusal microwear texture analysis. The modern groups are best differentiated on the basis of the level of complexity of their wear surfaces. To a lesser extent, the scale of maximum complexity, anisotropy, and texture fill volume were also differentiating factors. The results of this study show that surface complexity clearly distinguishes the groups based on the amount of hard objects included in their diets. The increase in surface complexity was found to be correlated with the increased ingestion of hard items. Scott et al. (2006) also found that surface complexity

was consistent with high bite force to fracture hard objects, as it served to arrange the four non-human primate groups analyzed (*Alouata palliata, Trachypithecus cristata, Lophocebus albigena,* and *Cebus apella*) in order of increasing *Asfc* in correlation with increasing ingestion of hard objects. The scale of maximum complexity appears to be linked to the scale of wear-causing particles (Scott et al. 2006). Small microwear features caused by small abrasive particles are detected at fine scale measurements and large features which are caused by large abrasive particles are detected at coarse scales. This variable differentiates the Fuegians, as having the highest *Smc*, and the Andamanese, as having the lowest *Smc*, from the other modern human groups considered. Anisotropy is linked to the directionality of the jaw movements during mastication (Scott et al. 2006). It serves to differentiate non-human primates with different diets since highly anisotropic surfaces are found among primates that consume more tough pliant items such as grasses and leaves (Scott et al. 2006; Scott et al. 2005). Because none of the modern human groups analyzed in this study had such a diet, anisotropy was not a strong differentiating factor in this case. The results of this study indicate that although anisotropy differentiates some of the groups, it does not give clear divisions according to either dietary habit or habitat. Scott et al. (2006) show that texture fill volume is greater in surfaces with larger deeper and more symmetrical areas of wear (i.e., heavily pitted surfaces). Texture fill volume differentiates the Ipiutak and Tigara, which included comparatively high amounts of hard objects, from the other modern human groups analyzed. This is expected, as hard object eaters have been shown to have highly pitted occlusal surfaces compared to those who have a mainly soft-object diet (e.g., Harman and Rose 1988; Teaford 1988; Teaford and Oyen 1989a; Teaford and Walker 1984). The

heterogeneity of surface texture is linked to the degree of variability in wear-causing particles ingested (Scott et al. 2006). This variable was not found to be a good differentiating factor among the modern groups analyzed in this study, suggesting that the modern human groups analyzed did not differ significantly in their degree of variability of hard particles ingested.

Fossil sample

Comparisons within the Neandertal sample

The primary goal of this study was to better understand the effects of ecogeographic variations on Neandertal dietary habits. These effects were tested by comparing the microwear signatures of samples that derive from the same region but from different oxygen isotope stages, and by comparing samples that date to the same oxygen isotope stage, but come from different regions. Although in some cases small sample sizes did not allow for statistical comparisons, differences in microwear signatures that correspond to differences in climatic reconstructions were still apparent. As was the case with the recent comparative baseline sample, microwear differences among the various fossil groups were related mostly to surface complexity.

Based on environmental conditions, the European Neandertals can be divided into two major groups, those that lived in cold-steppe vegetation (Subalyuk 1 and Guattari 3) and those that inhabited woodland environments (all of the other European Neandertals examined aside from Subalyuk 1, Guattari 3 and Spy 1). Unfortunately, the small sample

size of the European Neandertals from cold-steppe habitats (n=2) precluded statistical comparisons with other groups. However, it is apparent that the microwear signatures of the specimens from the open, cold-steppe environments are very different from those from wooded ones. The latter have more complex surfaces, which indicate a more abrasive diet. In comparison to the modern groups, the Neandertal specimens that derive from open-steppe environments exhibit microwear that most closely resembles that of the Fuegians (Figure 18). The open, steppe conditions in Europe during the cold glacial phases were most likely quite similar to those of Tierra del Fuego today. Such open environments support a low diversity of plant foods. Thus, it is possible that these ancient individuals relied more on meat than on plants under such climatic conditions, which would lead to less abrasive diets, as reflected in the low complexity of their microwear surfaces.

Smaller scale divisions were also seen among various Neandertal samples from the three different kinds of wooded habitats (Figure 18). Specimens were sampled from coniferous forests (i.e., central European specimens from St. Césaire, La Quina, and Vindija that date to OIS 3), deciduous woodlands (i.e., southern European specimens from the sites of Zafarraya, Sidrón and Breuil that date to OIS 3) and Mediterranean evergreen woodlands (i.e., southern European fossils from the site of Saccopastore dating to OIS 5e). Those that inhabited deciduous forest environments have more complex surfaces, implying a more abrasive diet, compared to those that lived in coniferous and Mediterranean evergreen forests. The specimen from Spy, which is the only one recovered from deposits indicative of shrub tundra vegetation, has a microwear signature that is close to the Neandertals from coniferous and Mediterranean evergreen woodlands.

The wear signatures of the Neandertals from coniferous and Mediterranean forests, in addition to those of Spy 1, are indistinguishable from those of the Chumash who lived under a Mediterranean climate (Figure 18). However, the microwear surfaces of the OIS 3 Neandertals from Southern Europe suggest that these individuals had a more varied diet compared to the other fossil specimens. The microwear fabrics of these southern European Neandertals resemble that of the Khoe-San, indicating that the amount of hard items ingested by these groups were similar (Figure 18). Paleoenvironmental reconstructions suggest that these Neandertals inhabited deciduous forest environments. Deciduous forests support a wide diversity of animal and plant species, which might explain the greater variability in the microwear fabrics of these individuals compared to the other Neandertals. The microwear signature of this group might suggest that they relied less on meat and more heavily on plant foods compared to the other Neandertals sampled here.

With regard to the Levantine Neandertals, Amud 1, who lived in a mix of deciduous and coniferous woodland vegetation (van Andel and Tzedakis 1996), has a microwear signature that places it with its European conspecifics that inhabited deciduous forest environments. They most closely resemble the Khoe-San among the modern groups (Figure 18). Kebara 2, on the other hand, lived under mixed woodland and semi-desert conditions (Cheddadi and Rossignol-Strick 1995), and has a microwear signature similar to European Neandertals from coniferous woodland environments. The microwear signature of Kebara 2 is closest to that of the Fuegians from the modern hunter-gatherers. A special note should be provided for the two Tabun specimens. Tabun 2 comes from layer C, which is considered to date to OIS 6 (Grün and Stringer 2000). At

this time, the Levant was covered with semi-desert vegetation (Cheddadi and Rossignol-Strick 1995). The microwear fabrics of Tabun 2 are most similar to Neandertals from coniferous forest environments. The stratigraphic position of Tabun 1, on the other hand, is debated. It is unclear whether Tabun 1 derives from layer C or the younger layer B (Alperson et al. 2000; Bar-Yosef and Callander 1999; Garrod and Bate 1937; Schwarcz et al. 1998). Tabun 1 has a higher level of surface complexity than Tabun 2, and is closer to the Neandertals from deciduous forest environments. This might suggest that Tabun 1 specimen lived under climatic conditions that were different from those at the time of deposition of Tabun 2, and this, in turn, might be taken as corroborative evidence that they come from different levels (Figure 18). This, however, remains a suggestion as small sample size precludes statistical analyses for the confirmation of these results.

None of the Neandertal groups have a microwear signature similar to those of the modern hunter-gatherers from Point Hope, Alaska and the Andaman Islands (Figure 18). This indicates that the diets of the Neandertals were not as abrasive as the diets of these modern groups. As noted above, the wear fabrics of these recent groups are most likely influenced by the indirect ingestion of abrasive particles attached to the dietary items as a result of food preparation techniques. The inclusion of such very high amounts of abrasives in the diet is not indicated for the Neandertals by their wear signatures. Also, although Neandertals sometimes inhabited cold and open environments, they did not face conditions as extreme as those of the arctic vegetation of modern Point Hope, Alaska.

Other lines of evidence have been used for the reconstruction of Neandertal diets. These include the analyses of stable isotopes, faunal and floral remains, and buccal microwear. Carbon and nitrogen stable isotopes have been extracted from a total of 12

Neandertal specimens derived from the six northern and central European sites of Les Pradelles, Saint Césaire, Scladina, Spy, Awirs and Vindija. Even though the carbon-nitrogen signatures of six of the twelve specimens might be slightly shifted due to chemical degradation (i.e., Les Pradelles 27801), carbon and nitrogen concentrations lower than those of fresh collagen (i.e., Les Pradelles M100), lack of baseline sample of associated faunal remains (i.e., Vindija Vi-207 and Vi-208 and Scladina MT500), or the effect of weaning (i.e., Awaris MT100), the carbon and nitrogen signatures average around -20‰ and 11.2‰ respectively and are thus consistent in identifying all the Neandertal specimens as top-level carnivores feeding mostly on terrestrial herbivores from open environments (1999; 2001; Bocherens and Drucker 2003; Bocherens et al. 2005; Bocherens et al. 1991; Fizet et al. 1995; Richards et al. 2000; Schoeninger 1982). The dental microwear analysis is in agreement with the results of the stable isotope analysis in classifying the northern and central European Neandertals as mainly meat eaters. However, in contrast to the stable isotope data, the results of the dental microwear analysis detect finer scale differences in the microwear signatures of Neandertal groups living under different environmental conditions (Figure 18). Although the specimens analyzed for stable isotopes are limited to northern and central Europe, and, with one exception, they all date to OIS 3, vegetational reconstructions indicate that the analyzed individuals were living under slightly different environments. These ranged from cold, steppic open environments (i.e., Les Pradelles) (Bocherens et al. 2005), to a shrub tundra vegetation (i.e., Spy and Awirs) (van Andel and Tzedakis 1996), to a mix of forest and steppe (i.e., Vindija) (Genty et al. 2005), to an open coniferous forest (i.e., St. Césaire) (van Andel and Tzedakis 1996). Differences in the microwear patterns of Neandertals

living under different conditions were detected. Indeed, the microwear fabric of the St. Césaire Neandertal that lived in an open coniferous forest differs from that of Subalyuk 1, which lived in an open, cold-steppe environment. The stable isotope signature of the St. Césaire Neandertal, however, was found to be very similar to those of the Les Pradelles specimens that lived in an open, cold steppe habitat similar to that of Subalyuk 1 (Bocherens et al. 2005). Moreover, although the microwear data identify the northern and central European Neandertals as having been mostly carnivorous, closely resembling recent humans from warmer climates that consume large amounts of meat (i.e., the Fuegians and the Chumash), the microwear patterns of the Neandertals from steppe environments most closely resemble those of modern Fuegians. The Neandertals from forested environments have wear fabrics most similar to the Chumash.

Wear fabrics also distinguish the Neandertals that lived in the deciduous forest environments of southern Europe during OIS 3 from the rest of the Neandertals, indicating that the former may not have relied as much on meat. Unfortunately, stable isotope data are not available for Neandertal specimens belonging to this group. In the light of the microwear data for this group, which suggests that they had a more mixed diet compared to the rest of the Neandertals analyzed, it would be interesting to establish whether their stable isotope signatures compare to those of Neandertals that were found to have a more carnivorous diet.

Several studies have recently summarized the evidence from Middle Paleolithic faunal assemblages from different parts of the European continent (Aura Tortosa et al. 2002; Boyle 2000; Patou-Mathis 2000). The results of these studies show that the Neandertals were effective hunters and that their hunting preferences varied by region

and oxygen isotope stage (Aura Tortosa et al. 2002; Boyle 2000; Patou-Mathis 2000). In northern and central Europe, the Neandertals mostly hunted large, open-environment herbivores (Patou-Mathis 2000). This is in agreement with the stable isotope data available for the specimens from these areas. However, during OIS 5e, the Neandertals selected medium-sized forest dwelling herbivores instead of the large open-habitat animals (Patou-Mathis 2000). Faunal assemblages from the middle latitudes of southwestern France and the Mediterranean sites indicate that the Neandertals were primarily hunting large quantities of medium-sized herbivores from both woodland and open habitats (Aura Tortosa et al. 2002; Boyle 2000). The Mediterranean areas also show a greater diversity of the species hunted (Aura Tortosa et al. 2002; Boyle 2000). Especially notable is the evidence from some Mediterranean sites for the exploitation of marine resources such as shellfish, including mollusks at Vanguard Cave and Devil's Tower, Gibraltar (Barton 2000; Bate 1928; Finlayson et al. 2001), and oysters, clams and mussels at Grotta di Moscerini, Italy (Stiner 1994), and maybe even marine mammals at Figueira Brava, Portugal (Antunes 2000). Such evidence is lacking from Neandertal sites from other parts of Europe. This evidence suggests a greater dietary breadth for these Mediterranean Neandertals compared to those from other parts of Europe. The microwear data support the notion of a greater diversity of the diets of the southern European Neandertals. However, the microwear data indicate that this diversity resulted from the ingestion of relatively greater amounts of abrasive objects, probably reflecting an increased reliance on hard plant foods, compared to Neandertals from other parts of Europe. Although some of the Neandertal specimens whose microwear signatures were analyzed in this study lived in close proximity to the sea (especially those from southern

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Europe), the distinction between a marine and terrestrial animal diet was not possible

using dental microwear. Meat is considered a low abrasive food and dental microwear

analysis primarily detects differences in the hardness/brittleness of the food ingested and,

with anisotropy, the toughness of these foods. Stable isotope analysis can differentiate

between aquatic and terrestrial diets (Katzenberg and Weber 1999; Schoeninger et al.

1983). The carbon and nitrogen signatures of all the Neandertal specimens examined to

date indicate a reliance on terrestrial rather than aquatic (marine and/or freshwater)

dietary resources, even though some of the specimens studied (i.e., Les Pradelles) lived

close to a riverine habitat (Balter and Simon in press; 1999; 2001; Bocherens and

Drucker 2003; Bocherens et al. 2005; Bocherens et al. 1991; Fizet et al. 1995; Richards et

al. 2000; Schoeninger 1982). It is unfortunate that stable isotope data from the southern

European Neandertals, especially those dating to OIS 3, are unavailable since both the

faunal and the microwear analyses point to a more diversified diet for this group

compared to those of other parts of Europe. Stable isotopes can give conclusive evidence

on whether the dietary diversity of the Mediterranean Neandertals resulted from a more

omnivorous diet and/or a diet including more marine resources compared to Neandertals

from other regions of Europe.

Studies of floral remains are still very limited and do not certainly serve to

provide meaningful inferences about Neandertal diets. These studies suggest that at

Kebara, the Neandertals collected legumes, wild grasses, fruits and seeds (Lev et al.

2005) and that at Amud they collected mature grasses for the consumption of their seeds

(Madella et al. 2002). Due to the lack of definite evidence for the dietary use of plants,

these must be considered loose inferences. These limited studies, however, suggest that

Neandertals were exploiting these plants, indicating that their diets were not exclusively based on meat. Floral remains are given more attention with modern excavation techniques, and with the excavation of new sites, a clearer picture of the Neandertals exploitation of plants might emerge.

Buccal microwear data have been collected from a number of European and Near Eastern Neandertals (Lalueza et al. 1996; Pérez-Pérez et al. 2003). However, as discussed above, sampling problems with the modern human baseline sample pose a significant problem for the interpretation of buccal microwear on fossil specimens. Nevertheless, the buccal microwear analyses indicate some degree of variability within the Neandertal sample. Variability in the occlusal microwear signatures within the sample of Neandertal was also detected. Pérez-Pérez et al. (2003) attempted a "preliminary analysis" of the relationship between buccal microwear density and climatic conditions, and their results indicate that for the period from OIS 2 to OIS 5, the Neandertals that date to interglacial periods have lower buccal microwear density, indicating a less abrasive diet, than those that date to glacial periods. However, as the authors point out, the buccal microwear data from their OIS 6 Neandertal sample, which has the lowest mean striation density among all the other groups, contradicts this pattern. Thus, detailed comparisons between the buccal and occlusal microwear data await the publication of more in-depth analysis of the correlation between Neandertal buccal microwear and ecogeographic variations.

Comparisons between the Neandertals and other fossil groups

The Pre-Neandertals also lived through the changing environments of the Ice Age, and these changes affected their dietary habits as reflected by their microwear signatures. Thus, the specimens that derive from wooded environments (Atapuerca – Sima de los Huesos, Steinheim and Pontnewydd) present different microwear fabrics from those that inhabited open-steppe environments (Arago, Montmaurin and Mauer). As was found among the various Neandertal groups, the Pre-Neandertal specimens recovered from more open environmental conditions have less complex surfaces (and, thus, presumably less abrasive diets) compared to those from wooded/forested environments. It is not possible to dissect more finely the effects of different kinds of forest environments on the microwear pattern of the Pre-Neandertal specimens because the paleoenvironmental reconstructions indicate that all of these fossils were recovered from coniferous forests. In comparison to the modern groups included in this study, the Pre-Neandertal specimens that derive from open-steppe environments exhibit microwear that most closely resembles that of the Fuegians (Figure 18). The fossils that come from forested environments resemble the Chumash (Figure 18).

The differences in the microwear signatures between specimens from wooded and steppe environments indicate that both the Neandertals and their predecessors were flexible in their dietary habits, and were able to adapt to new environments. Dental microwear suggests that the dietary shifts between environments in the Neandertals and Pre-Neandertals were similar to one another. The two Neandertal specimens (Guattari 3 and Subalyuk 1) who inhabited steppe conditions have a microwear signature similar to those of Pre-Neandertals from steppe conditions. Thus, when environments became more open/steppic, they both showed a reduction in the level of surface complexity.

Environments with open vegetation support a lower variety of plant species than do wooded environments, and the lower complexity in the microwear signature of the specimens from open environments would appear to reflect a reduction in hard plant food items and potentially an increased reliance on meat (which, by itself, does not cause abrasion on occlusal molar surfaces). When the vegetation was more wooded, food variety, especially plants, increased and thus there was a greater possibility of eating hard objects such as seeds and nuts, thereby increasing the complexity of the microwear surface texture. There are currently no stable isotope data available for Pre-Neandertal specimens to speak to these inferences.

Unfortunately, only one specimen, Skhul 7, among the "anatomically modern" human fossils from Skhul and Qafzeh preserved antemortem microwear. Therefore, meaningful comparisons between it and the Neandertal samples from different climatic conditions are not possible. It can only be said that Skhul 7, which lived in a wooded environment, has a microwear signature closest to that of Neandertals from deciduous forest environments. As discussed above, the Neandertals from the deciduous forests were found to have the greatest level of surface complexity compared to other Neandertal groups. Thus, the results of this study indicate that Skhul 7 had a diet similar to the Neandertals from the deciduous forests, which was more varied compared to the other Neandertal groups.

The early Upper Paleolithic specimens (sample of 15) that date to OIS 3 come from coniferous woodland environments that were either open or had some steppe elements. These specimens range rather widely in microwear surface texture complexity, and variability is exhibited even by specimens from a single site, such as Barma Grande

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and Dolni Vestonice. This suggests some dietary variability among these individuals. They inhabited a mix of coniferous forest and steppe environments that probably yielded a variety of different foods. The early Upper Paleolithic specimens have microwear signatures similar to those of both the Chumash and Fuegians. The range of surface complexity values among the early Upper Paleolithic individuals encompasses those of Pre-Neandertal, "anatomically modern" (i.e., Skhul 7), and all of the Neandertal specimens analyzed, except those from the southern European deciduous forests of OIS 3.

Evidence of a more diversified diet of Upper Paleolithic humans compared to the Neandertals is also available from stable isotope analyses and supported by archaeological finds from early and mid Upper Paleolithic contexts. Stable isotope data are available from ten Upper Paleolithic specimens from northern, central and southern European and west-central Asian that date to between 27-20 kyr (with the exception of Kostenki, which dates to 33 kyr (Pettitt et al. 2003; Richards et al. 2001)). The δ^{13}C values for these Upper Paleolithic humans range between -18.4‰ and -19.2‰, and their δ^{15}N values range between 9.3‰ and 15.3‰ (Pettitt et al. 2003; Richards et al. 2001). These values indicate an omnivorous rather than carnivorous diet, which also included small animal prey and aquatic (freshwater or marine depending on the site locations) foods (Pettitt et al. 2003; Richards et al. 2001). These stable isotope results contrast with those of the northern and central European Neandertals, whose carbon and nitrogen values indicate their diets to have been dominated by large to medium size terrestrial herbivores, and to have lacked aquatic species (1999; 2001; Bocherens and Drucker 2003; Bocherens et al. 2005; Bocherens et al. 1991; Fizet et al. 1995; Richards et al.

2000; Schoeninger 1982). Although the faunal analyses indicate that some coastal Neandertals, mostly those from southern Europe, occasionally exploited some kinds of marine fish and shellfish (Antunes 2000; Barton 2000; Bate 1928; Finlayson et al. 2001; Stiner 1994), the degree of such exploitation remains to be examined using stable isotope analyses. Archaeological and stable isotope evidence for the exploitation of freshwater aquatic resources is lacking from Middle Paleolithic contexts. The Les Pradelles specimens, for example, lived near an inland riverine habitat, yet their stable isotope data do not show the consumption of aquatic resources (Bocherens et al. 2005).

Archaeological evidence supports a greater dietary breadth for the Upper Paleolithic humans compared to the Neandertals. Grinding stones are found at several Upper Paleolithic sites (e.g., at Dolni Vestonice and Kostenki and several sites in the Rhineland) probably suggesting a greater reliance on plant foods (Svoboda et al. 2000). Such evidence is typically absent from the Middle Paleolithic. Moreover, evidence for the increased exploitation of fish comes from various Upper Paleolithic sites, such as Hohle Fels and Geissenklősterle in Germany (Bosinski 2000; Hahn 2000) and La Riera in northern Spain (Straus and Clark 1986). Although fish remains are found in few Middle Paleolithic contexts, mostly from southern Europe, these suggest an occasional exploitation of such resources. Bird remains are also found in greater numbers in Upper Paleolithic contexts (e.g., Pavlov I) (Svoboda et al. 2000). In southern Greece, for example, the site of Franchthi Cave shows an increase in consumption of shellfish, fish, and plant during the early Upper Paleolithic compared to the Middle Paleolithic (Perlès 2000). Also, unlike the Neandertals, the faunal remains show a greater exploitation of small animals by Upper Paleolithic humans.

The three lines of evidence discussed here, microwear analyses, stable isotope analyses and archaeological data, all support a more diversified diet for the early Upper Paleolithic humans compared to northern and central European Neandertals. Taken together, these data describe the Neandertal's diets as having lacked diversity, focusing on meat from large to medium sized terrestrial herbivores. In contrast, various lines of evidence indicate that early Upper Paleolithic humans from all over Europe had a more omnivorous diet, including a greater amount of plant foods, small animal prey and aquatic resources. Thus, if the Upper Paleolithic humans in Europe had a wide range of dietary habits, as suggested by various dietary reconstruction techniques including microwear analysis, competition over dietary resources with Neandertals would likely have been unavoidable. This, in turn, might suggest support for the possibility that modern humans competed with the Neandertals for resources, and played a role in their disappearance.

However, the microwear and archaeological data differentiate the southern European Neandertals (especially those dating to OIS 3) as having a more diverse diet compared to those inhabiting the northern and central regions of the continent. The results of faunal analyses indicate a greater diversity in prey selection and the exploitation of some marine resources by southern European Neandertals. The results of the microwear analysis suggest that the Neandertals dating to OIS 3 from southern Europe (i.e., Zafarraya, Sidron 1 and 2 and Breuil 2) and the Levant (i.e., Amud 1), as a group, had microwear signatures that were significantly different from those of the other Neandertals analyzed, including those from northern and central Europe, in having greater surface complexity indicating more varied diets. Microwear analyses also

distinguish this southern European and Levantine Neandertal group from the early Upper Paleolithic humans. This distinction suggests that the dietary habits of the early Upper Paleolithic humans, although encompassing those of most European and Levantine Neandertal groups, were probably different from at least some of the Mediterranean Neandertals living during OIS 3. Moreover, the microwear signatures of the early Upper Paleolithic specimens are indistinguishable from those of some, but not all, of the late surviving Neandertals (e.g., St. Césaire, Zafarraya, and Breuil). The level of surface complexity of the St. Césaire and Zafarraya Neandertals fall within the range of values of the early Upper Paleolithic humans, whereas the value for the Breuil specimen falls outside this range. This suggests dietary similarity –possibly equivalence – between early Upper Paleolithic individuals and some, but not all, of the late surviving Neandertals. Thus, this evidence might be used to argue against dietary competition between Neandertals and early modern humans as a cause for Neandertal extinction. However, it should be kept in mind that the Neandertal specimens examined in this study do not temporally overlap the early Upper Paleolithic fossils that were studied here. Thus, the microwear signatures of the geochronologically youngest Neandertals included here would not reflect possible changes in dietary habits that might have resulted from the arrival of modern humans in Europe. Therefore, testing the hypothesis of competition between Neandertal and early Upper Paleolithic humans over dietary resources awaits the analysis of late-surviving Neandertals that overlapped the earliest modern humans in Europe.

Chapter 9

Conclusion

This study had four goals: 1) to document the microwear signatures of modern human groups with known and diverse dietary habits, 2) to better understand the effects of ecogeographic variations on Neandertal dietary habits, 3) to compare the microwear signatures of Neandertals with those of fossil hominins that predated and postdated them in Europe, and with those of their contemporaries in the Levant, and 4) to infer the dietary proclivities of the Neandertals and the other fossil groups by comparison with the recent human samples. These goals were successfully achieved through the study of occlusal dental microwear texture analysis.

First, the microwear fabrics of seven modern hunter-gatherer groups with varied dietary habits were documented to better understand how dietary differences affect microwear in these groups and to establish a reasonable comparative database to interpret microwear in Late Pleistocene humans. The modern hunter-gatherer samples were selected from historic and prehistoric populations that represent: 1) carnivorous hunter-gatherers from arctic/tundra environments (Ipiutak, Tigara and Aleutian Islanders), 2) mixed diet hunter-gatherers from tropical climates (Khoe-San and Andamanese), and 3) carnivorous hunter-gatherers from relatively warm climates (Fuegians and Chumash). Microwear differences between the carnivorous hunter-gatherers and the mixed diet hunter-gatherers were detected, and significant differences were also found among the carnivorous hunter-gatherers that inhabited different environments. To this end, the

microwear fabrics of the Ipiutak, Tigara and Andaman Islanders reflect the highly abrasive diet of these individuals, which is most likely related to the ingestion of hard particles clinging to their foods as a result of their food preparation techniques (i.e., drying the meat on open racks on the sandy beaches of Point Hope, Alaska for the Ipiutak and Tigara, and cooking the food uncovered allowing windborne sand particles to be included with it for the Andamanese). The microwear signatures of the Chumash and Fuegians, on the other hand, classify them as having the least abrasive diet among the modern groups. This is expected, as the dietary habits of Chumash and Fuegians consisted mostly of meat from marine animals, which by themselves are too soft to indent the enamel surface. Also, there is no indication in the ethnohistoric accounts that these two groups ingested any kind of extraneous abrasive particles. Significant differences in the microwear signatures between the Fuegians and Chumash were also detected reflecting subtle dietary differences, probably related to a somewhat greater amount of hard plant foods eaten by the Chumash. The mixed diet Khoe-San and the Aleutian Islanders, the mostly meat eaters from the arctic, occupy an intermediate position between the two Point Hope populations and the Andamanese on the one hand and the Chumash and Fuegians on the other, with regard to the level of abrasives ingested. The mixed diet of the Khoe-San included large amounts of plant foods, such as nuts, seeds, tubers, that were most likely responsible for abrading their enamel surface. The microwear signature of the Aleuts is most likely a reflection of their high meat intake coupled with the ingestion of attached grit particles. However, the amount of grit ingested by the Aleutian Islanders is not as excessive as that of the Point Hope populations and the Andamanese Islanders.

The second goal, to understand the effects of climatic change on the dietary habits of the Neandertals, was met by comparing the microwear signatures of Neandertals from a given geographic area that derived from glacial and interglacial periods, and by comparing microwear patterns among Neandertal groups that dated to the same time period, but derived from different geographical areas. Dental microwear texture analysis detected variations in the Neandertal signatures that almost certainly correspond to dietary habits that differed in response to ecogeographic changes. Neandertals that inhabited open steppe environments exhibit less surface complexity than those that lived in wooded environments. Differences among Neandertals that inhabited various kinds of woodland/forest environments were also detected. Those that lived in deciduous forests have greater surface complexity than those that lived in coniferous and Mediterranean forest environs, suggesting that the former had a more abrasive diet.

In fulfillment of the third goal of this study, the microwear signatures of Neandertals were compared with those of the Pre-Neandertals from Europe, the early Upper Paleolithic specimens from Europe and one early "anatomically modern" human from the Levant. The results indicate that climatic change had an effect on Pre-Neandertals microwear. Like the Neandertals, the Pre-Neandertals from open steppe environments had a lower level of surface complexity than those from wooded environments. The microwear evidence suggests that the Neandertals and their predecessors responded similarly to the changes in vegetation cover.

Unfortunately, meaningful statistical comparisons between the Neandertals and early "anatomically modern" humans from the Levant are not possible because microwear data were successfully recovered only from Skhul 7. However, the microwear

signature of this specimen places it among the OIS 3 Neandertals from the deciduous forests of southern Europe that were found to have a relatively more abrasive diet compared to the rest of the Neandertal fossils examined.

The early Upper Paleolithic human sample exhibits a wide range of microwear surface complexity values, reflecting a wide range of dietary items that were chewed. The range of surface complexity of this sample encompasses the values of all other fossil specimens with the exception of those from the deciduous forests of southern Europe that date to OIS 3.

The final goal of this study was to examine possible differences in the dietary habits of the various fossil human samples through the analysis of their microwear signatures. Apart from the Neandertals that inhabited the deciduous forests of southern Europe during OIS 3, all the fossil samples had microwear fabrics similar to those of recent meat-eaters from relatively warm environments, i.e., the Fuegians and Chumash. The Neandertals and Pre-Neandertals that lived in open steppe environments have microwear signatures similar to those of the Fuegians, who also inhabited an open steppe environment. The Neandertals and Pre-Neandertals that lived in coniferous and Mediterranean woodland environments have wear fabrics similar to those of the Chumash, who also occupy a wooded environment. It can therefore be argued that when environments were more wooded, the Neandertals and Pre-Neandertals, who relied mostly on meat for their subsistence, also included more plant foods and hard objects in their diets than when environments were open steppe. The Neandertals that inhabited the deciduous forests of southern Europe during OIS 3 had more varied diets and probably did not rely as much on meat as the other Neandertal groups. The microwear signature of

this Neandertal group is most similar to those of modern mixed-diet hunter-gatherers (the Khoe-San). The results of this study show that Neandertals cannot be considered as a single, homogenous sample in terms of their behaviors because they seem to have had significant dietary differences. The microwear signatures of the early Upper Paleolithic specimens are indistinguishable from the Fuegians and Chumash, which probably reflects a more varied diet for this group.

All the Neandertal specimens that have been examined to date for stable isotopes are indicated to have been top level carnivores, obtaining their meat mostly from terrestrial rather than aquatic (marine and freshwater) animals. Carbon and nitrogen data are still limited, however, to northern and central European Neandertals that, with the exception of two specimens, all date to OIS 3. The results of the faunal analyses from northern and central European sites support a low diversity in the diets of these Neandertals and indicate that their diets relied mostly on large to medium-size terrestrial herbivores. The microwear data are in accord with the stable isotope data in identifying the northern and central European Neandertals as mostly meat eaters. However, the dental microwear analysis was able to detect divisions among the Neandertal groups from these regions at a finer scale, especially between those that inhabited open-steppe environments and those that lived in forested habitats. Thus, subtle differences in the dietary habits of the different Neandertal groups were observed, whereas stable isotope analyses have not been able to detect such differences.

The results of this study suggest that the OIS 3 Neandertals from southern Europe had a more diverse diet, probably including more plants, compared to those of other Neandertal specimens examined. Faunal analyses support this dietary diversification by

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providing evidence for the exploitation of marine resources and small animal prey by these Neandertals. There are no records of stable isotopes recovered from southern European Neandertals. Since stable isotope analysis has the potential to differentiate between carnivorous and omnivorous diets, and between the sources of meat, i.e., terrestrial versus aquatic, included in the diet, it would be interesting to establish how the stable isotope signatures of these southern European Neandertals compare to those of other groups that were found to have a more carnivorous diet. Moreover, evidence from stable isotopes, faunal remains and occlusal microwear show that the diets of early Upper Paleolithic humans were more diverse compared to those of northern and central European Neandertals. The results of the microwear analysis also show that the early Upper Paleolithic humans had microwear signatures encompassing all of Neandertal groups with the exception of those from the OIS 3 of southern Europe. Thus, the extraction of stable isotopes from southern European Neandertals might also shed light on the significant differences found between the microwear signatures of the southern European OIS 3 Neandertals and the early Upper Paleolithic humans.

Finally, the results of this study demonstrate the ability of dental microwear texture analysis to reveal subtle differences in the dietary habits of modern and fossil humans.

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Table 1. Some animal species expected to be found in different vegetation areas of Eurasia (after Musil 1985). X = present

Species	Tundra	Subarctic Forest/Taiga	Steppe + Arctic/Loess Steppe	Mild Zone Forest/ Meadows
Alces alces		X	X	
Alopex lagopus	X		X	
Alactaga jaculus			X	
Bison priscus			X	
Bos primigenius		X		X
Canis lupus		X		X
Capreolus capreolus				X
Castor fiber		X		X
Cervus elaphus		X		X
Citellus citellus			X	
Citellus rufescens			X	
Coelodonta antiquitatis	X		X	
Cricetus cricetus			X	
Dama dama				X
Dicerorhinus hemitoechus			X	
Dicrostonyx torquatus	X			
Dicrostonyx henseli	X			
Equus hydruntinus			X	
Equus hemionus			X	
Equus sp.			X	
Felis silvestris				X
Glis glis				X
Gulo gulo	X			
Lemmus lemmus	X			
Lepus timidus	X		X	
Lutra lutra				X
Lynx lynx		X		X
Mammuthus primigenius	X		X	
Marmota marmota		X	X	
Martes foina				X
Martes martes				X
Megaloceros giganteus		X	X	
Ochotona pusilla			X	
Oryctolagus cuniculus				X
Ovibos moschatus	X		X	
Panthera leo				X
Rangifer tarandus	X	X	X	
Saiga tatarica			X	

Table 1. *Continued*

Species	Tundra	Subarctic Forest/Taiga	Steppe + Arctic/Loess Steppe	Mild Zone Forest/ Meadows
Sciurus vulgaris		X		X
Spermophilus rufescens			X	
Sus scrofa				X
Ursus arctis		X		
Ursus arctos				X
Ursus priscus				X
Vormela sp.			X	
Vulpes vulpes				X

Table 2. Stable isotopes (carbon-nitrogen) signatures from bone collagen for Neandertals and associated fauna.

Site	Species	Analysis number	$\delta^{13}C$	$\delta^{15}N$	Reference
Les Pradelles					
	Neandertals				
		27801	-20.2	9.3	Bocherens et al. 1991
		64801	-19.1	11.6	Fizet et al. 1995
		M300	-19.1	11.5	Bocherens et al. 2005
		M400	-19.5	11.4	
		M100	-21.8	8.4	
	Fauna				
	Bos primigenius				
			-20.6	6.3	Bocherens et al. 1991
			-20.1	6.3	Bocherens et al. 1991
			-20.0	6.4	Bocherens et al. 1991
			-20.0	6.3	Bocherens et al. 1991
	Bison priscus				
			-20.1	6.3	Fizet et al. 1995
			-19.9	8.1	Fizet et al. 1995
			-19.9	7.5	Fizet et al. 1995
			-19.7	6.3	Fizet et al. 1995
			-19.8	5.9	Fizet et al. 1995
	Rangifer tarandus				
			-20.2	0.9	Bocherens et al. 1991
			-19.7	3.1	Bocherens et al. 1991
			-19.9	3.3	Bocherens et al. 1991
			-20.1	6.1	Bocherens et al. 1991
			-19.0	3.5	Bocherens et al. 1991
			-19.5	2.6	Fizet et al. 1995
			-19.7	3.1	Fizet et al. 1995
			-19.9	3.3	Fizet et al. 1995
			-20.4	4.4	Fizet et al. 1995
			-20.2	4.2	Fizet et al. 1995
			-19.7	5.5	Fizet et al. 1995
			-19.2	3.8	Fizet et al. 1995
			-19.5	3.9	Fizet et al. 1995
			-19.6	4.6	Fizet et al. 1995
			-19.6	4.4	Fizet et al. 1995
	Equus caballus germanicus				
			-20.5	5.0	Bocherens et al. 1991
			-20.8	4.8	Bocherens et al. 1991
			-20.5	6.0	Bocherens et al. 1991
			-20.1	4.9	Fizet et al. 1995
			-20.7	4.8	Fizet et al. 1995

		-20.5	5.0	Fizet et al. 1995
		-21.0	5.1	Fizet et al. 1995
		-20.5	4.8	Fizet et al. 1995
		-20.8	4.8	Fizet et al. 1995
		-20.3	3.6	Fizet et al. 1995
		-21.9	7.9	Fizet et al. 1995
		-20.7	6.8	Fizet et al. 1995
		-20.4	5.5	Fizet et al. 1995
		-20.7	5.9	Fizet et al. 1995
		-22.2	6.4	Fizet et al. 1995
		-20.4	7.4	Fizet et al. 1995
		-19.2	3.9	Fizet et al. 1995
		-21.4	6.3	Fizet et al. 1995
		-20.4	2.3	Fizet et al. 1995
		-20.6	5.5	Fizet et al. 1995
Marmola marmota				
		-21.8	4.0	Bocherens et al. 1991
		-21.8	4.0	Fizet et al. 1995
Canis lupus				
		-18.5	9.6	Bocherens et al. 1991
		-18.8	12.1	Fizet et al. 1995
		-18.5	9.6	Fizet et al. 1995
		-18.6	9.4	Fizet et al. 1995
Vulpes vulpes				
		-20.0	8.6	Bocherens et al. 1991
		-20.0	8.6	Fizet et al. 1995
		-19.6	8.2	Fizet et al. 1995
Crocuta crocuta spaelea				
		-19.5	10.3	Bocherens et al. 1991
Crocuta splaea				
		-19.6	10.3	Fizet et al. 1995
Saint Césaire				
Neandertals				
	RPB7000	-19.8	11.4	Bocherens & Drucker 2003
Fauna				
Bos or Bison				
		-20.9	6.1	Bocherens et al. 2005
Rangifer tarandus				
		-18.8	4.9	Bocherens et al. 2005
		-18.3	7.3	Bocherens et al. 2005
Megaloceros giganteus				
		-20.5	5.0	Bocherens et al. 2005

Table 2. *Continued*

Site	Species	Analysis number	δ¹³C	δ¹⁵N	Reference
La Barbie					
	Fauna				
	Bison priscus				
			-20.3	6.1	Bocherens et al. 2005
			-20.1	5.6	Bocherens et al. 2005
			-20.8	4.7	Bocherens et al. 2005
			-20.3	5.6	Bocherens et al. 2005
			-20.2	6.1	Bocherens et al. 2005
			-20.2	6.0	Bocherens et al. 2005
			-20.9	4.6	Bocherens et al. 2005
			-20.5	5.3	Bocherens et al. 2005
	Rangifer tarandus				
			-19.2	3.7	Bocherens et al. 2005
			-19.4	3.9	Bocherens et al. 2005
			-19.1	7.6	Bocherens et al. 2005
			-19.4	5.8	Bocherens et al. 2005
	Equus caballus				
			-20.4	7.5	Bocherens et al. 2005
			-20.9	3.5	Bocherens et al. 2005
	Coelodonta antiquitatis				
			-19.6	7.2	Bocherens et al. 2005
	Mammuthus primigenius				
			-21.8	8.5	Bocherens et al. 2005
			-19.9	9.5	Bocherens et al. 2005
			-19.1	8.5	Bocherens et al. 2005
			-19.1	9.8	Bocherens et al. 2005
Camiac					
	Fauna				
	cf. *Bos primigenius*				
			-20.0	6.1	Bocherens et al. 2005
			-20.7	6.2	Bocherens et al. 2005
			-20.4	7.4	Bocherens et al. 2005
			-20.1	8.6	Bocherens et al. 2005
			-20.0	6.0	Bocherens et al. 2005
			-20.4	5.3	Bocherens et al. 2005
	Megaloceros giganteus				
			-20.0	6.4	Bocherens et al. 2005
			-20.1	7.7	Bocherens et al. 2005
	Cervus elaphus				
			-20.0	6.9	Bocherens et al. 2005
			-20.6	6.2	Bocherens et al. 2005
	Equus caballus				
			-20.7	5.2	Bocherens et al. 2005

Site	Species	Analysis number	$\delta^{13}C$	$\delta^{15}N$	Reference
	Equus caballus				
			-20.5	5.2	Bocherens et al. 2005
	Coelodonta antiquitatis				
			-19.9	8.4	Bocherens et al. 2005
	Coelodonta antiquitatis				
			-20.1	7.1	Bocherens et al. 2005
			-20.6	7.1	Bocherens et al. 2005
	Mammuthus primigenius				
			-21.2	8.7	Bocherens et al. 2005
			-21.8	7.7	Bocherens et al. 2005
	Crocuta crocuta				
			-19.3	9.8	Bocherens et al. 2005
			19.0	9.1	Bocherens et al. 2005
Scladina					
	Neandertals				
		MT500	-21.2	11.8	Bocherens et al. 2001
		SC18800	-19.9	10.9	Bocherens et al. 1999
	Fauna				
	Rangifer tarandus				
			-18.7	3.1	Bocherens et al. 2001
	Equus sp.				
			-21.2	4.1	Bocherens et al. 2001
	Equus caballus				
			-25.1	5.6	Bocherens et al. 1999
	Dama dama				
			-23.3	8.2	Bocherens et al. 1999
			-22.3	7.3	Bocherens et al. 1999
			-22.6	9.7	Bocherens et al. 1999
			-22.8	7.2	Bocherens et al. 1999
			-23.9	8.2	Bocherens et al. 1999
			-21.8	7	Bocherens et al. 1999
			-23.1	7.2	Bocherens et al. 1999
			-22.9	6.8	Bocherens et al. 1999
			-22.4	6.4	Bocherens et al. 1999
	Ursus spelaeus				
			-22.2	5.4	Bocherens et al. 2001
			-23.3	3.7	Bocherens et al. 1999
			-23.1	3	Bocherens et al. 1999
			-23	3.3	Bocherens et al. 1999
			-23.6	4.5	Bocherens et al. 1999
	Ursus arctos				
			-18.6	4.8	Bocherens et al. 1999
			-22	4.7	Bocherens et al. 1999

Table 2. *Continued*

Site	Species	Analysis number	$\delta^{13}C$	$\delta^{15}N$	Reference
	Vulpes vulpes				
			-19.5	5.8	Bocherens et al. 1999
			-19.4	5.6	Bocherens et al. 1999
			-19.3	7.3	Bocherens et al. 1999
			-19.5	7.1	Bocherens et al. 1999
	Alopex lagopus				
			-19.7	7	Bocherens et al. 1999
			-19.5	5.6	Bocherens et al. 1999
	Panthera Leo spelaea				
			-19.2	10.3	Bocherens et al. 1999
	Crocuta crocuta spelaea				
			-20.3	8.9	Bocherens et al. 1999
			-21.1	7.9	Bocherens et al. 1999
	Canis lupus				
			-20.2	7.6	Bocherens et al. 1999
Awirs Cave					
	Neandertals				
		MT100	-19.6	12.6	Bocherens et al. 2001
Spy Cave					
	Neandertals				
		MT200	-19.8	11.0	Bocherens et al. 2001
Vindija					
	Neandertals				
		Vi-207	-19.5	10.1	Richards et al. 2000
		Vi-208	-20.5	10.8	Richards et al. 2000
	Fauna				
	Bos/Bison spp.				
			-20.4	5.3	Richards et al. 2000
	Cervid				
			-20.3	5.2	Richards et al. 2000
	Ursus spelaeus				
			-21.1	1.3	Richards et al. 2000
			-20.7	1.5	Richards et al. 2000

Table 3. Fossil specimens examined for this study.

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Group	Site	Individual Number	Tooth	Date in kyr	Dating Method	OIS	Geographical Area	Vegetation Cover
Pre-Neandertals								
	Mauer	1	RM_2	735-640	Geological	16-18	Central Europe	Steppe/Tundra**
	Arago	13	RM_1					
		21	RM^1	450	U-series	12	Southern Europe	Arid-Cold Steppe
		54	RM^1					
	Steinheim	1	RM^1	~225 or 325*	Faunal Association	7 or 9	Central Europe	Woodland
	Sima de los Huesos	3	RM^2					
		4	RM^1					
		7	LM^2					
		8	RM^1	>200*	ESR/U-Series	>7	Southern Europe	Coniferous Woodland
		17	RM^1					
		19	LM^2					
		22	RM^1					
	Pontnewydd	1	RM^2	~200	TL dating	7	Northern Europe	Coniferous Forest**
		12	LM^1					
	Montmaurin	Mandible	RM_1	~130	Floral and faunal association	6	Central Europe	Steppe with some tree refugia
Neandertals								
	Tabun	1	RM^1	165-102*	ESR	6-5*	Levant	Semi-desert if OIS 6 and Wooded if OIS 5**
		2	LM_2	165-130	ESR and TL	6		Semi-desert**

Table 3. *Continued*

Group	Site	Individual Number	Tooth	Date in kyr	Dating Method	OIS	Geographical Area	Vegetation Cover
	Saccopastore	1 2	LM^2 RM^2	130-120	Faunal Association	5e	Southern Europe	Mediterranean Evergreen Woodland **
	Guattari	3	RM$_2$	74-60	U-series and ESR	4	Southern Europe	Arid Cold Steppe**
	Subalyuk	1	LM$_2$	70-60	Faunal Association	4	Central Europe	Steppe
	Kebara	2	LM$_2$	64-60	TL and ESR	4-3	Levant	A mix of woodland and Semi-desert**
	Amud	1	RM$_2$	55-53	TL, ESR and Th/U	3	Levant	Mix Coniferous and Deciduous Forest**
	La Quina	5 20	RM^2 LM^2	48-40	TL	3	Central Europe	Steppe with some coniferous trees **
	Sidrón	1 2	LM$_1$ LM$_2$	44-42	Radiocarbon	3	Southern Europe	Coniferous Woodland**
	Vindija	11.39 11.45 11.46 11.409 12.1	RM$_1$ LM$_2$ LM^1 LM$_1$ RM^2	42	Radiocarbon	3	Central Europe	Coniferous Forest**
	Spy	1	RM^2	40-35	Faunal association	3	Northern Europe	Shrub tundra**
	Breuil	2	LM$_1$	37	ESR	3	Southern Europe	Deciduous Woodland**
	St. Césaire	1	RM^1	36	TL	3	Central Europe	Open Coniferous Forest**

Table 3. *Continued*

Group	Site	Individual Number	Tooth	Date in kyr	Dating Method	OIS	Geographical Area	Vegetation Cover
	Zafarraya		RM_1	33	U-series	3	Southern Europe	Deciduous Woodland
	Ochoz	1	LM_1		Faunal Association	5 or 3	Central Europe	Unavailable
Anatomically Modern								
	Skhul	7	LM_2	~100*	ESR, U-series, TL	5d-5a	Levant	Wooded**
Early Upper Paleolithic								
	Mladeč	1	RM^1					
		2	LM^1	31	Radiocarbon	3	Central Europe	Forest-steppe**
		4	LM^1					
		8	LM^2					
	Stetten	1	RM_2	31	Radiocarbon	3	Central Europe	Open Coniferous Forest**
	Combe Capelle	1	RM^2	28-25	Archaeological Association	3	Central Europe	Open Coniferous Forest**
	Předmostí	Mandible	RM_1	26	Radiocarbon	3	Central Europe	Forest-steppe
	Pavlov	3	RM_2	26	Radiocarbon	3	Central Europe	Coniferous Forest
	Dolni Věstonice	13	RM^1	26				
		14	RM_1		Radiocarbon	3	Central Europe	Forest-steppe
		16	LM_2	29-26				
		31	RM_1					
	Barma Grande	1	LM_2					
		2	RM_2	26-23	Radiocarbon	3	Southern Europe	Steppe with some coniferous trees**
		5	RM^2					

* Refer to text for details.

** Since no direct paleoclimatic and paleovegetation data is available for these sites, conditions during these times are inferred. See text for details.

Table 4. Descriptive statistics for *Asfc, smc, epLsar*, and *HAsfc* for modern specimens

	N	Asfc		Smc		epLsar		HAsfc		Tfv	
		Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Ipiutak	20	9.961	7.460	0.189	0.033	0.0025	0.0014	0.418	0.569	5309.55	2475.66
Tigara	24	6.924	5.644	0.221	0.093	0.0032	0.0013	0.401	0.353	4596.13	2753.55
Aleut	19	3.247	1.696	0.271	0.199	0.0029	0.0010	0.477	0.401	6994.09	795.26
Andamanese	29	7.110	4.454	0.184	0.093	0.0026	0.0011	0.337	0.223	6938.75	1347.27
Khoe-San	46	4.050	2.369	0.198	0.051	0.0026	0.0012	0.393	0.291	6947.08	989.79
Chumash	11	1.955	0.917	0.227	0.086	0.0024	0.0008	0.217	0.132	6949.82	976.34
Fuegians	6	1.048	0.267	0.387	0.116	0.0043	0.0014	0.230	0.098	5936.50	1771.87

Table 5. Results of statistical analysis for the modern samples.

A. MANOVA results

		F	Hypothesis df	Error df	P
Wilks' Lambda	0.071	375.9149	5	144	0.00
Pillai's Trace	0.929	375.9149	5	144	0.00
Hotelling's Trace	13.053	375.9149	5	144	0.00

B. Individual ANOVAS

		Sum of Squares	df	Mean Square	F	P
Asfc	Effect	100605.9	6	16767.6	11.8	0.000
	Error	209704.1	148	1416.9		
Smc	Effect	59259.3	6	9876.5	5.8	0.000
	Error	251050.2	148	1696.3		
epLsar	Effect	31725.0	6	5287.5	2.8	0.013
	Error	278585.0	148	1882.3		
HAsfc	Effect	18624.4	6	3104.1	1.6	0.158
	Error	291685.6	148	1970.8		
Tfv	Effect	46942.7	6	7823.8	4.4	0.000
	Error	263366.8	148	1779.5		

C. Multiple comparisons tests (matrices of pairwise mean differences)

		Aleut	Ipiutak	Tigara	Andamanese	Khoe-San	Chumash
Ipiutak							
	Asfc	50.4‡					
	Smc	3.0					
	epLsar	24.0					
	TFV	28.2†					
Tigara	*Asfc*	32.7‡	17.7				
	Smc	2.7	5.7				
	epLsar	4.0	28.0†				
	TFV	43.6‡	15.4				
Andamanese							
	Asfc	42.3‡	8.1	9.6			
	Smc	37.3‡	34.3†	40.0‡			
	epLsar	21.1	2.9	25.1			
	TFV	1.7	29.9†	45.3‡			
Khoe-San							
	Asfc	12.2	38.2‡	40.5‡	30.1‡		
	Smc	5.5	2.5	8.2	31.7‡		
	epLsar	17.5	6.5	21.5	3.6		
	TFV	0.4	28.6†	44.0‡	1.3		
Chumash							
	Asfc	27.0†	77.4‡	59.7‡	69.3‡	39.2‡	
	Smc	7.8	10.8	5.1	45.1‡	13.4	

Table 5 C. *Continued*

		Aleut	Ipiutak	Tigara	Andamanese	Khoe-San	Chumash
	epLsar	24.0	0.1	28.0	2.8	6.5	
	TFV	0.5	27.7	43.0†	2.3	0.9	
Fuegians							
	Asfc	49.7‡	100.2‡	82.5‡	92.0‡	61.9‡	22.7†
	Smc	60.0‡	63.0‡	57.3‡	97.2‡	65.5‡	52.1†
	epLsar	37.3	61.3‡	33.3	58.4‡	54.8†	61.3†
	TFV	26.2	2.0	17.4	27.9	26.6	25.6

† Fisher's LSD test *p*≤0.05
‡ Fisher's LSD and Tukey's HSD test *p*≤0.05

Table 6. Descriptive statistics for the fossil sample.

	N	Asfc		Smc		epLsar		HAsfc		Tfv	
		Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Pre-Neandertals – wooded	10	2.43	0.94	6.04	12.18	0.0026	0.00076	0.47	0.40	6634.28	1603.074
Pre-Neandertal – Steppe	5	0.98	0.32	30.23	36.95	0.0036	0.00094	0.25	0.14	6895.415	1151.767
Central Europe OIS 3	8	1.47	0.37	0.79	1.13	0.0024	0.00058	0.26	0.14	6437.523	812.3197
Southern Europe OIS 3	4	3.61	1.25	2.38	4.39	0.0029	0.00145	0.38	0.44	7003.229	809.4133
Upper Paleolithic	15	1.83	1.28	19.722	61.00	0.0026	0.00090	0.25	0.13	6779.985	1323.217

Table 7. Results of statistical analysis for the fossil samples.

A. MANOVA results

	F		Hypothesis df	Error df	P.
Wilks' Lambda	0.032	194.312	5	33	0.000
Pillai's Trace	0.967	194.312	5	33	0.000
Hotelling's Trace	29.441	194.312	5	33	0.000

B. Individual ANOVAS

		Sum of Squares	df	Mean Square	F	P
Asfc	Effect	2303.842	4	575.9604	5.511357	0.001389
	Error	3866.658	37	104.5043		
Smc	Effect	676.9667	4	169.2417	1.139875	0.352957
	Error	5493.533	37	148.4739		
epLsar	Effect	953.5167	4	238.3792	1.690638	0.172895
	Error	5216.983	37	140.9995		
HAsfc	Effect	309.7417	4	77.43542	0.488863	0.743827
	Error	5860.758	37	158.3989		
Tfv	Effect	155.675	4	38.91875	0.239407	0.914219
	Error	6014.825	37	162.5628		

C. Multiple comparisons tests (matrices of pairwise mean differences)

		Pre-Neandertals – woodland	Pre-Neandertal – Steppe	Central Europe OIS 3	Southern Europe OIS 3
Pre-Neandertal – Steppe	*Asfc*	19.50‡			
Central Europe OIS 3	*Asfc*	9.98	9.53‡		
Southern Europe OIS 3	*Asfc*	8.15	27.65‡	18.13‡	
Early Upper Paleolithic	*Asfc*	8.83	10.67	1.14	16.98‡

† Fisher's LSD test *p*≤0.05
‡ Fisher's LSD and Tukey's HSD test *p*≤0.05

Table 8. Results of statistical analysis for the modern vs. the fossil samples.

A. MANOVA results

		F	Hypothesis df	Error df	P
Wilks' Lambda	0.184	160.715	5	181	0.000
Pillai's Trace	0.816	160.715	5	181	0.000
Hotelling's Trace	4.439	160.715	5	181	0.000

B. Individual ANOVAS

		Sum of Squares	df	Mean Square	F	P
Asfc	Effect	293095.7	11	26645.07	14.329	0.000
	Error	344002.3	185	1859.47		
Smc	Effect	184659.5	11	16787.23	6.864	0.000
	Error	452437.5	185	2445.61		
epLsar	Effect	70721.62	11	6429.24	2.100	0.022
	Error	566375.9	185	3061.49		
HAsfc	Effect	43197.1	11	3927.01	1.223	0.274
	Error	593900.9	185	3210.28		
Tfv	Effect	86490.09	11	7862.74	2.642	0.054
	Error	550607.4	185	2976.26		

C. Multiple comparisons tests (matrices of pairwise mean differences)

	Pre-Neandertals – woodland	Pre-Neandertal – Steppe	Central Europe OIS 3	Southern Europe OIS 3	Early Upper Paleolithic
Ipiutak					
Asfc	77.30‡	132.40‡	110.88‡	44.25	100.73‡
Smc	58.00†	84.00‡	31.83	32.45†	50.57†
epLsar	11.10	68.60†	1.16	18.40	15.87
Tigara					
Asfc	56.68‡	111.77‡	90.25‡	23.63	80.11‡
Smc	50.18†	76.18†	24.00	24.63†	42.74†
epLsar	25.55	31.95	37.81	24.25	20.78
Aleut					
Asfc	18.72	73.82‡	52.29‡	14.33	42.15‡
Smc	52.83†	78.83†	26.65	27.28†	45.39†
epLsar	20.88	36.62	33.14	19.58	16.11
Andamanese					
Asfc	69.06‡	124.16‡	102.63‡	36.00	92.49‡
Smc	96.28‡	122.28‡	70.11‡	70.73†	88.85‡
epLsar	7.39	64.89†	4.87	8.69	12.16
Khoe-San					
Asfc	34.06‡	89.16‡	67.63‡	1.01	57.49‡
Smc	60.45‡	86.45‡	34.27	34.90	53.02‡
epLsar	1.95	59.45†	10.31	3.25	6.72

Table 8 C. *Continued*

	Pre-Neandertals – woodland	Pre-Neandertal – Steppe	Central Europe OIS 3	Southern Europe OIS 3	Early Upper Paleolithic
Chumash					
Asfc	16.52	38.58‡	17.06	49.56†	6.92
Smc	44.53	70.53†	18.35	18.98	37.09
epLsar	10.97	68.47†	1.29	12.27	15.73
Fuegians					
Asfc	51.87†	3.23	18.29†	84.92‡	28.43
Smc	18.37	7.63	44.54	43.92	25.80
epLsar	69.13†	11.63	81.39†	67.83	64.37†

† Fisher's LSD test $p \leq 0.05$
‡ Fisher's LSD and Tukey's HSD test $p \leq 0.05$

Table 9. Microwear data collected using the SEM and MICROWARE for the Ipiutak, Tigara and Aleutian Islanders.

	Ipiutak n=22	Tigara n=27	Aleut n=23
Percent Pitting			
Mean	41.44	56.34	43.25
SD	8.50	6.75	8.63
Feature Tally			
Mean	157.80	254.61	133.65
SD	34.49	59.16	31.73
Scratch Breadth			
Mean	1.32	1.17	1.54
SD	0.20	0.18	0.21
Pit Width			
Mean	3.10	3.22	3.33
SD	0.83	0.51	0.74
Pit Length			
Mean	5.26	5.17	5.61
SD	1.24	0.83	1.37

Table 10. F values for the pair-wise ANOVA comparisons among the Ipiutak, Tigara and Aleutian Islanders analyzed. Microwear data was collected using the SEM and MICROWARE.

	Ipiutak F	Tigara F
Aleut		
Pit Percentage	0.47	34.08†
Feature Tally	5.54†	68.70†
Scratch Breadth	11.783†	41.15†
Pit Width	0.88	0.37
Pit Length	0.76	1.88

† = significant difference $p < 0.05$

Figure 1. The main European sites yielding long pollen sequences.

Figure 2. Reconstructions of the vegitation cover in Europe and the Levant at different stages. A) Vegetation cover that would have existed in Europe today in the absence of agriculture; B) during OIS 6 at 150 kyr; C) during OIS 5e at 120-125; D) during OIS 4 at 65 kyr; E) during a warm phase of OIS 3 at 39-36 kyr. All reconstructions are after van Andel and Tzedakis (1996).
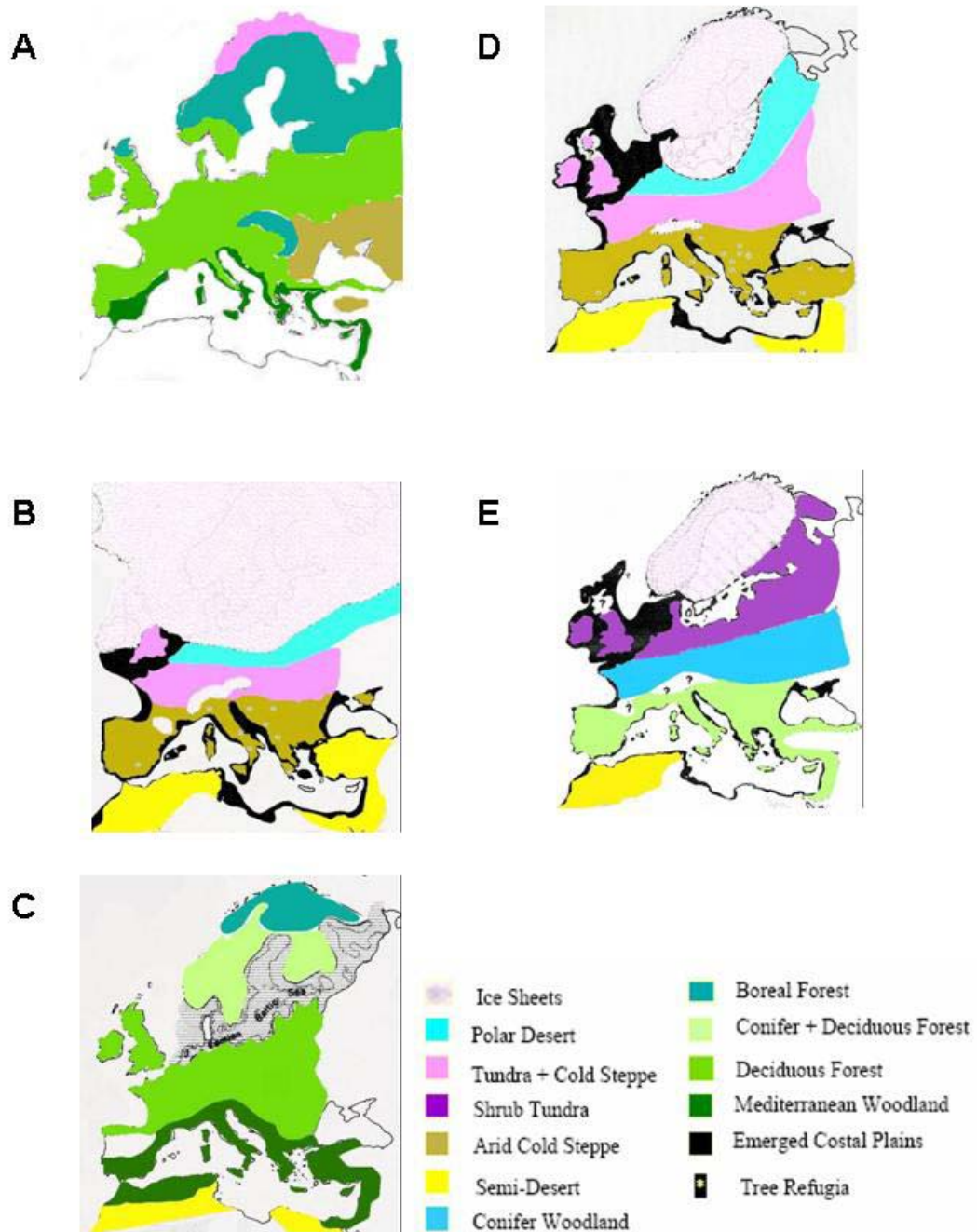
Figure 3. Oxygen isotope curve from the deep-sea core V19-30 located in the Pacific Ocean. Dates on the left are in kyr. This figure is adapted from Klein (1999).
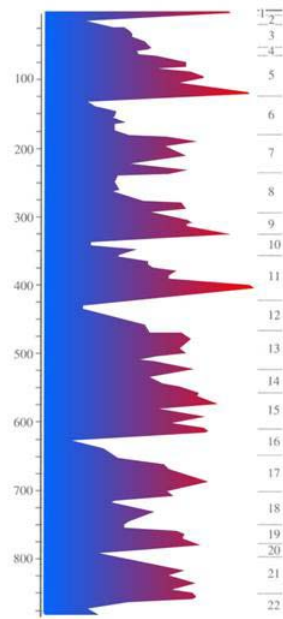
Figure 4. Stable isotopes (carbon-nitrogen) isotopic signatures from bone collagen for Neandertals and their associated fauna. Herbivores are in green, carnivores in red, and omnivores in purple. Neandertals are represented in blue.
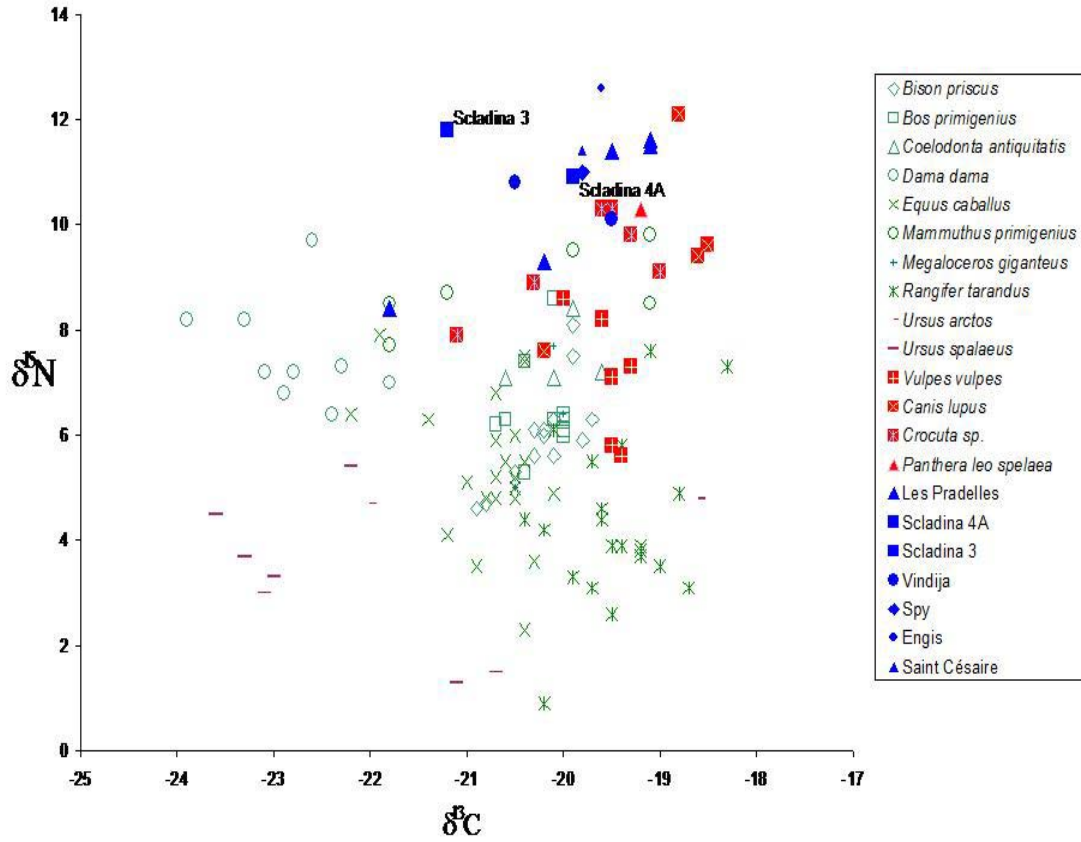
Figure 5. Map showing the location of the sites yielding dental remains included in this study.
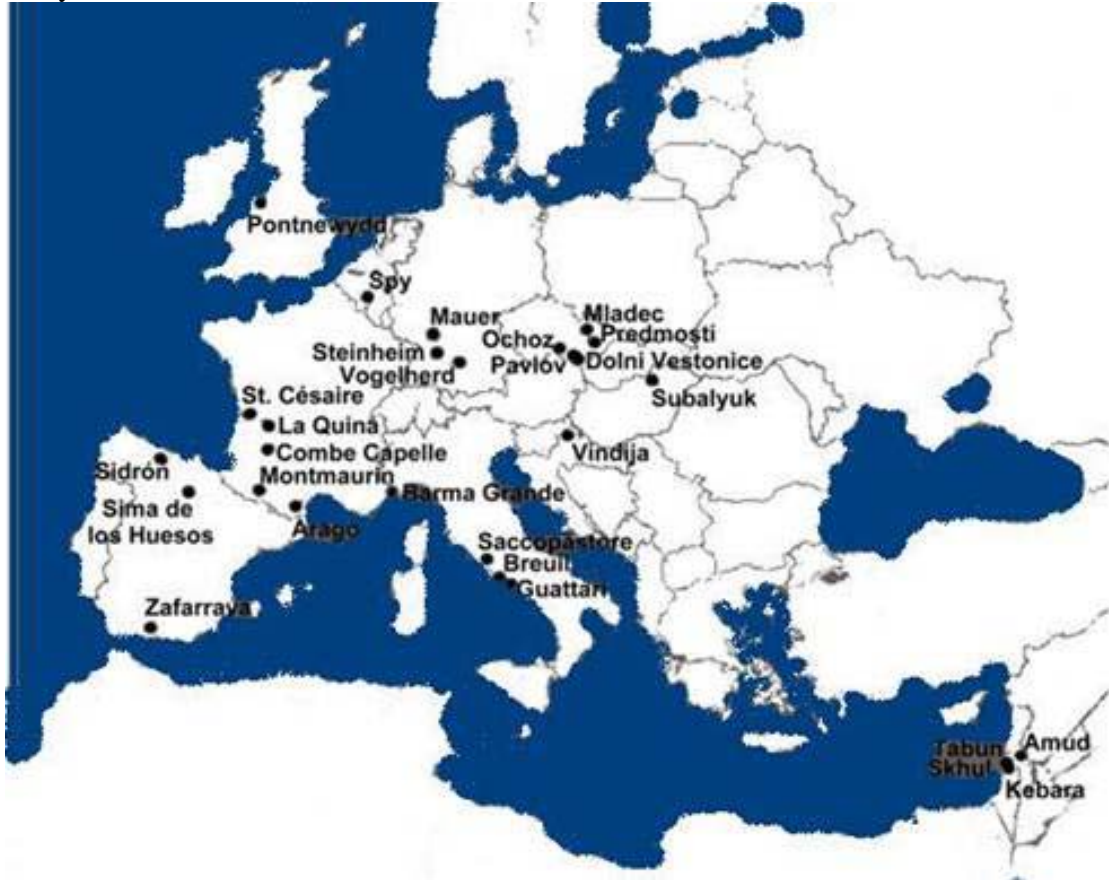
Figure 6. Examples of artifacts and actual wear surfaces: A) and B) surfaces covered with glue taken at 10 and 100x magnification respectively, C) surface (taken at 10x) covered with bubbles as a result of poor casting, D) artifact resulting from a sharp tool having scratched the surface during specimen preparation (20x), E) surface covered with dirt (100x), F) and G) "good" surfaces (100x).
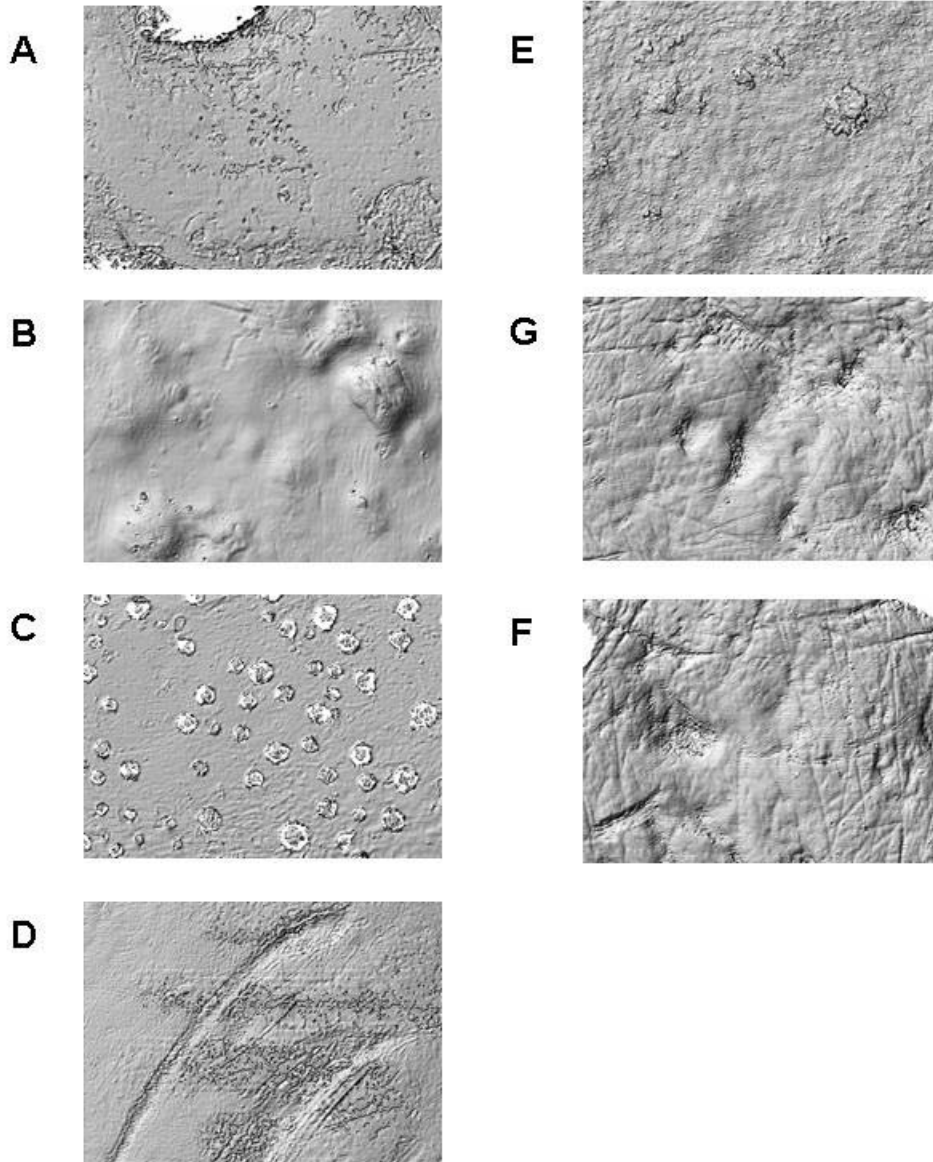
Figure 7. A-C) Examples of change in relative area of a surface as result of change in the scale of observation. D) represents the measure of complexity. Adapted from Scott et al. (2005).
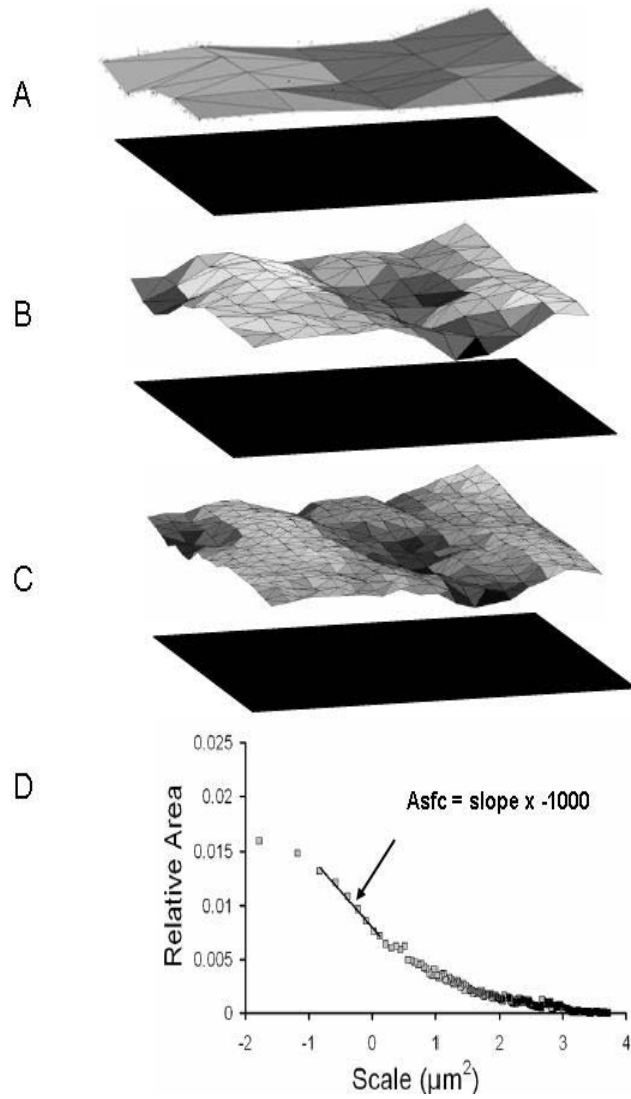
Figure 8. Examples of surfaces with high (A) and low (B) complexity. Highly complex surface (A) are surfaces that have a lot of microwear features overlying each other, and the opposite is true for surfaces of low complexity (B).
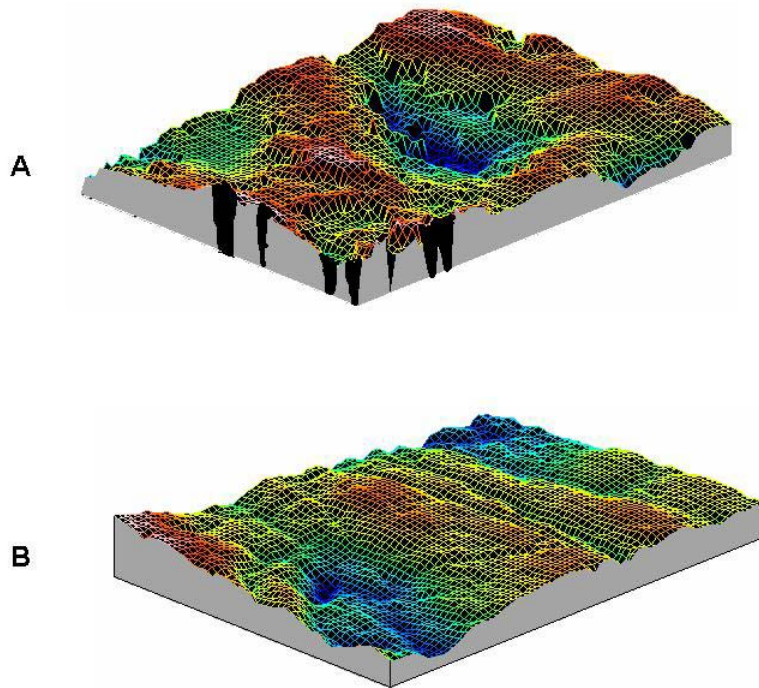
Figure 9. Examples of microwear surfaces with high (A) and low (B) anisotropy represented. Surfaces with high anisotropic (A) are surfaces with a lot of parallel scratches compared to low anisotropic surfaces (A).
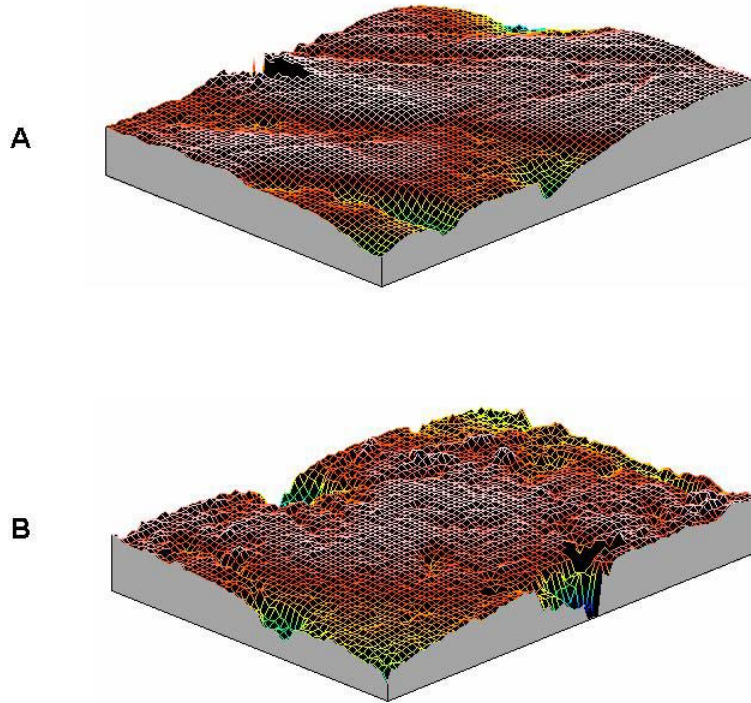
Figure 10. The changes in relative length of a profile with changes in the scale of observation (A-B). Length profiles can be measured at different orientations (C). The rosette plot of relative lengths taken at 36 different orientations (D). Adapted from Scott et al. (2005).
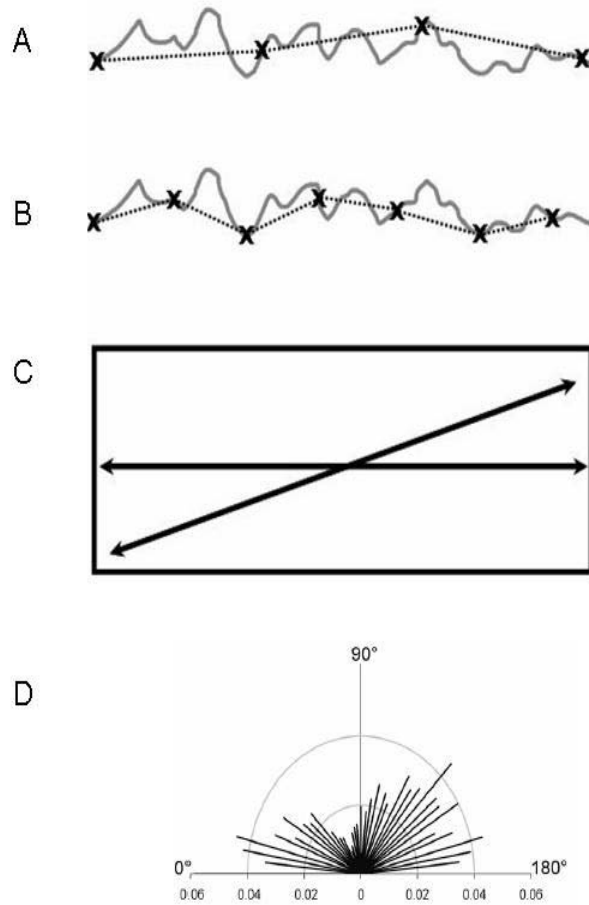
Figure 11. Changes in structural fill volume with changes in the scale of measurement. Adapted from Scott et al. 2005.
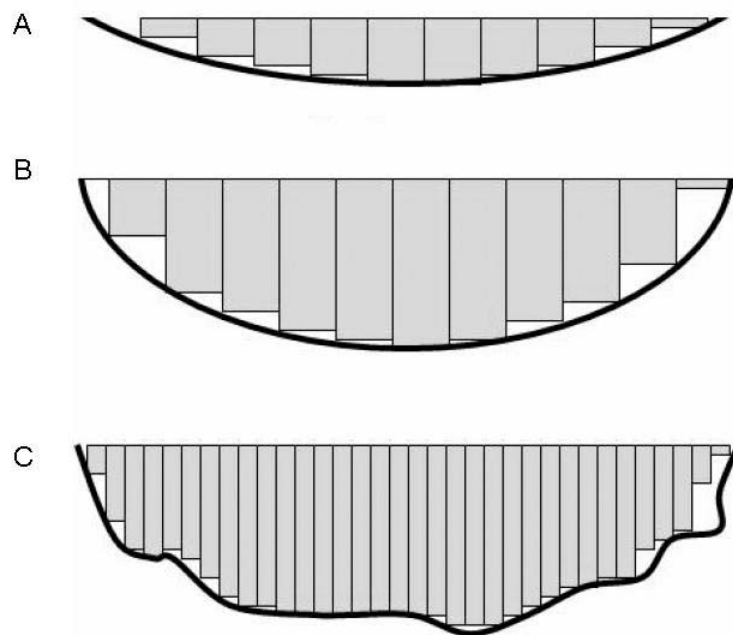
Figure 12. Representative micrographs of the modern human groups. A) Fuegians, B) Chumash, C) Khoe-San, D) Aleutian Islanders, E) Ipiutak, F) Tigara, and G) Andamanese.

E

F

G

H
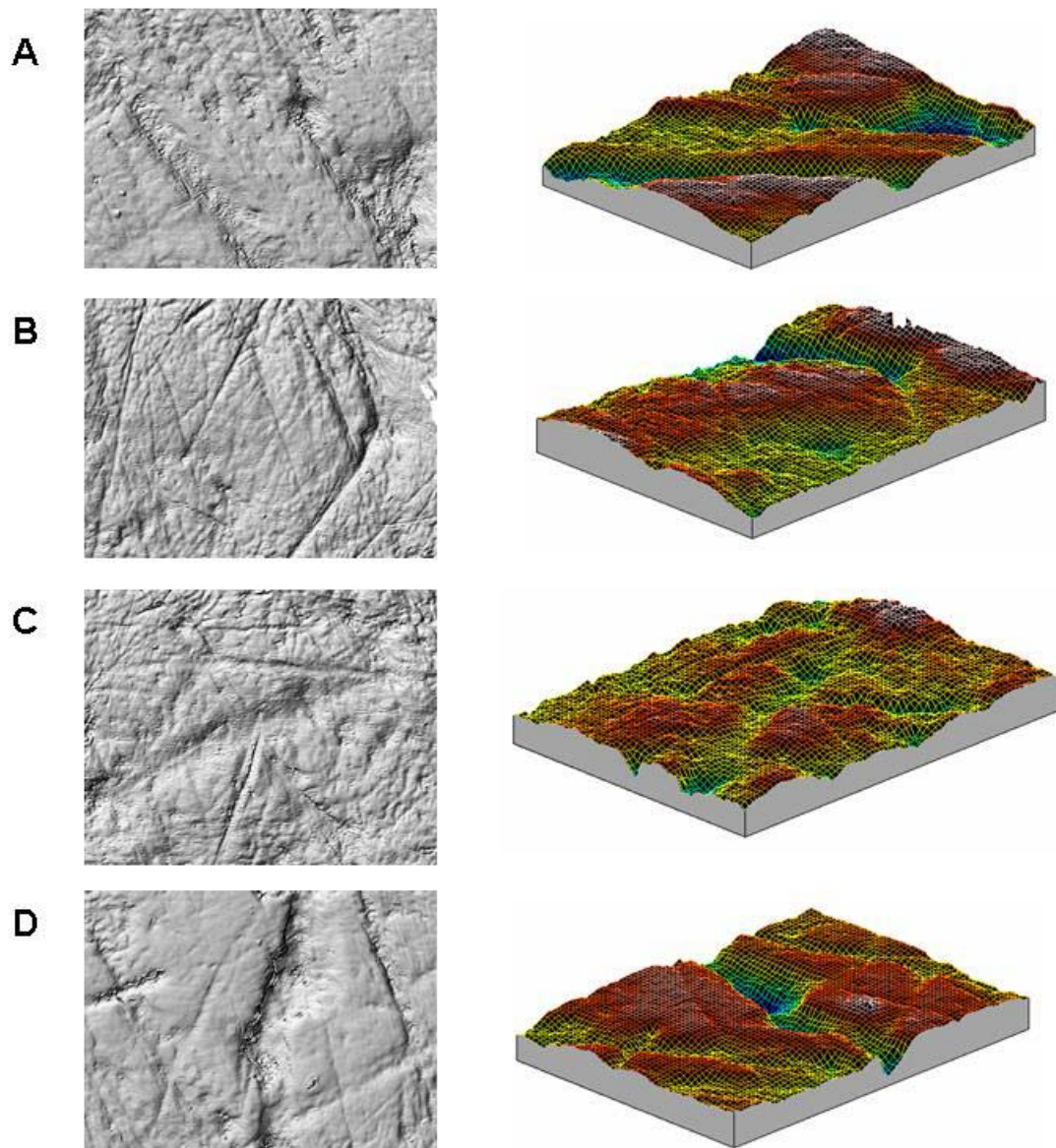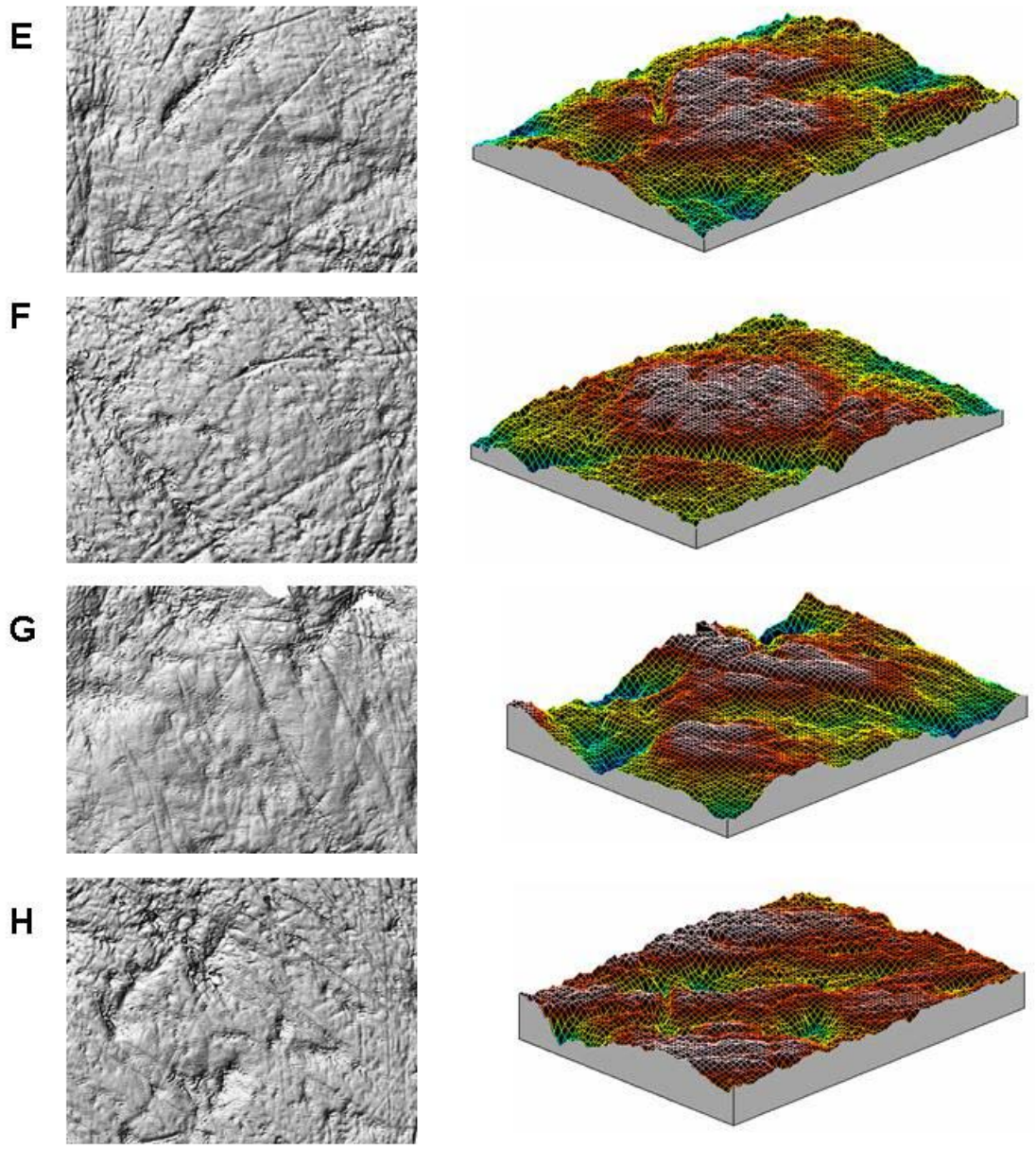
Figure 13. Representative micrographs of the fossil groups. A) Atapuerca – Sima de los Huesos individual 7, B) Steinheim, C) Arago 21, D) Montmaurin, E) Breuil 2, F) La Quina 5, G) Vindija 11.45, H) Subalyuk 1, I) Guattari 3, J) Tabun 1, K) Tabun 2, L) Skhul 7, M) Mladec 2, N) Barma Grande 1, and O) Dolni Vestonice 13.

F

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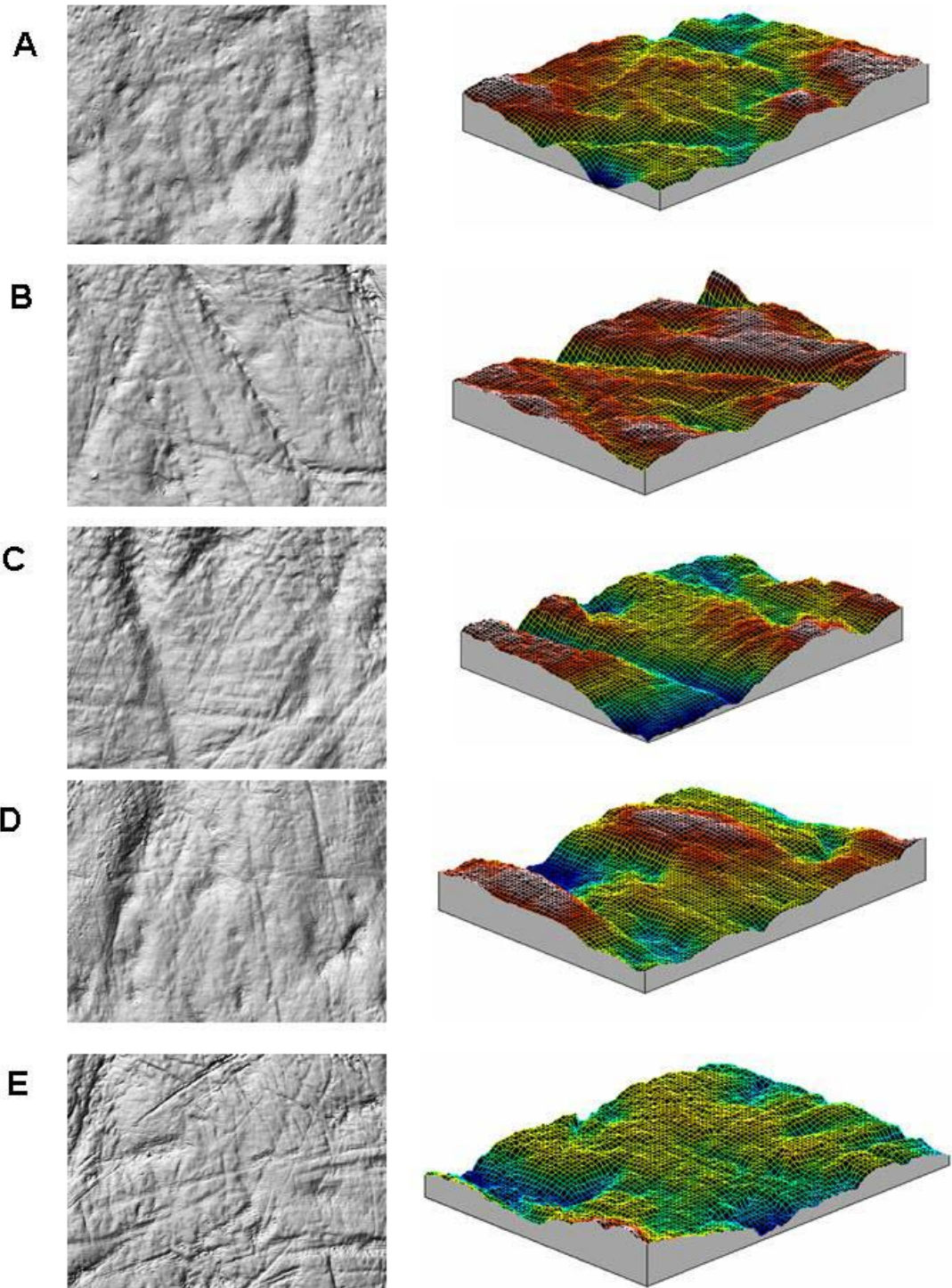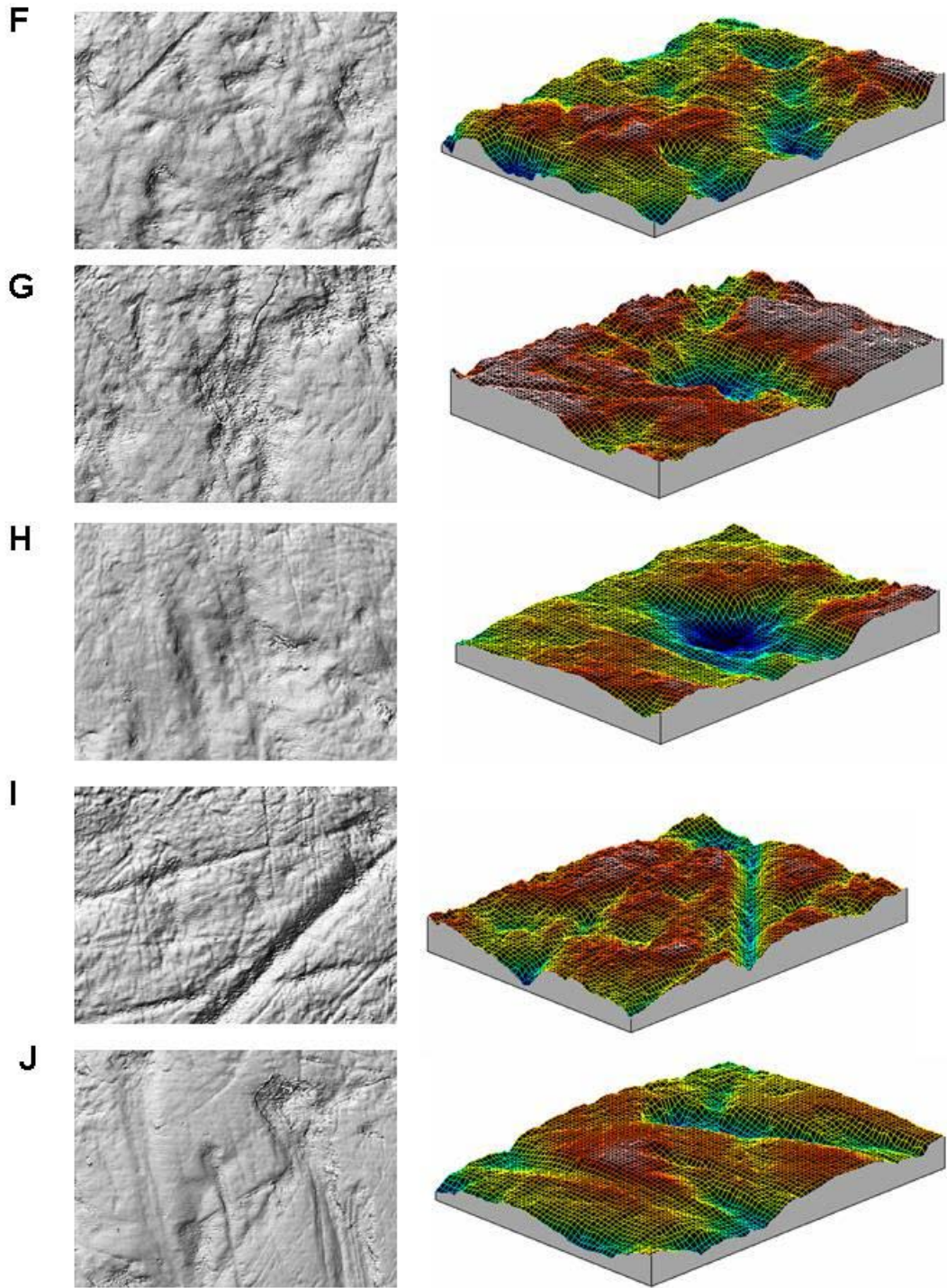
K
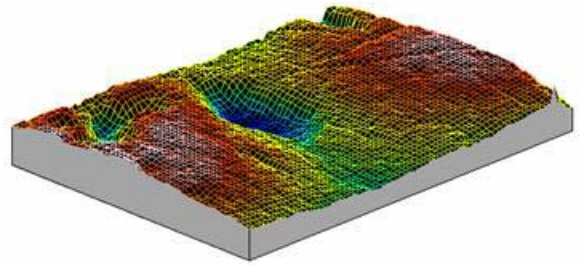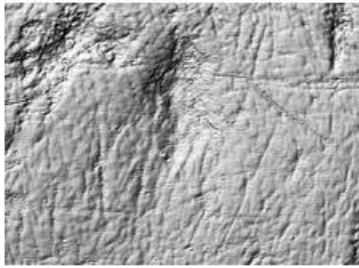
L
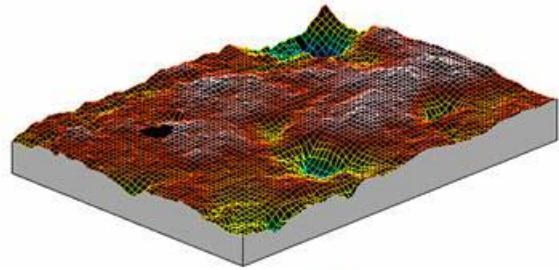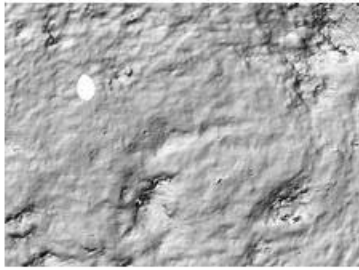
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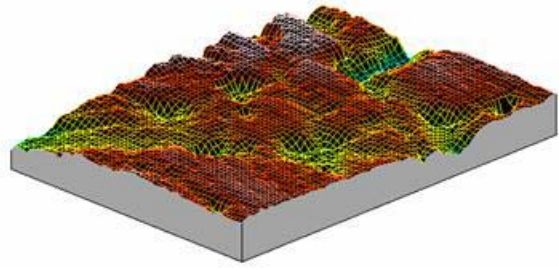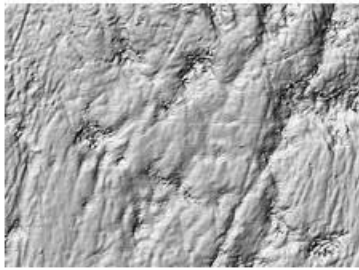
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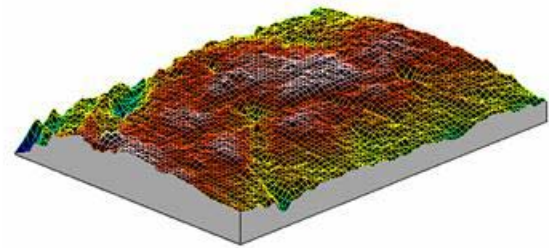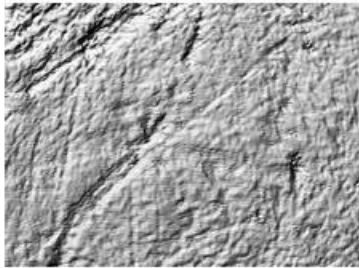
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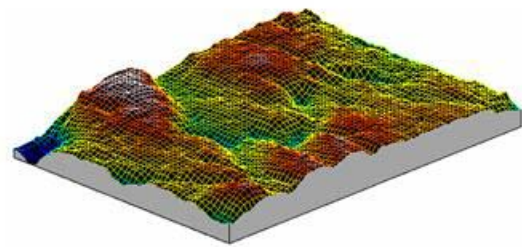
Figure 14. Summary statistics for the modern human groups. A) *Asfc*, B) *Smc* C) *epLsar,* and D) *Tfv*. Circles= sample means, horizontal lines = ±1 SD of the mean. Blue represents the carnivorous hunter-gatherers from the arctic, green represents the mixed diet hunter-gatherers from the tropics, and red represents the carnivorous hunter-gatherers from warmer climates.
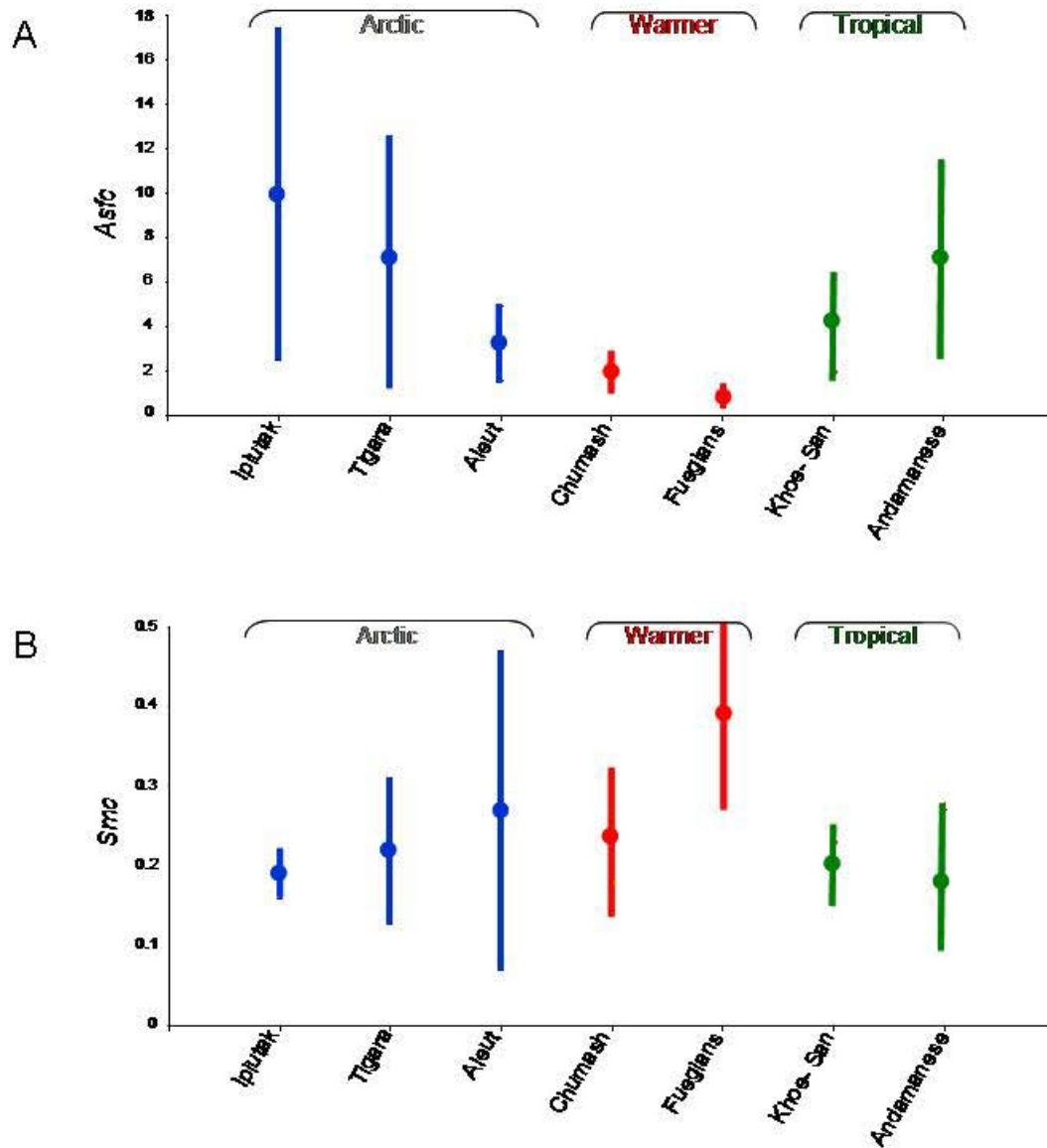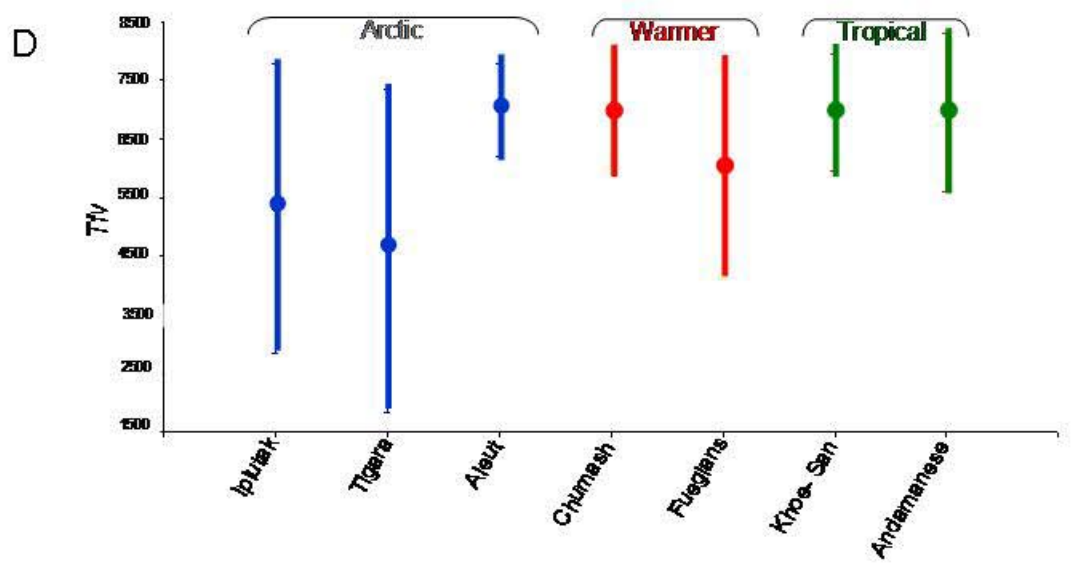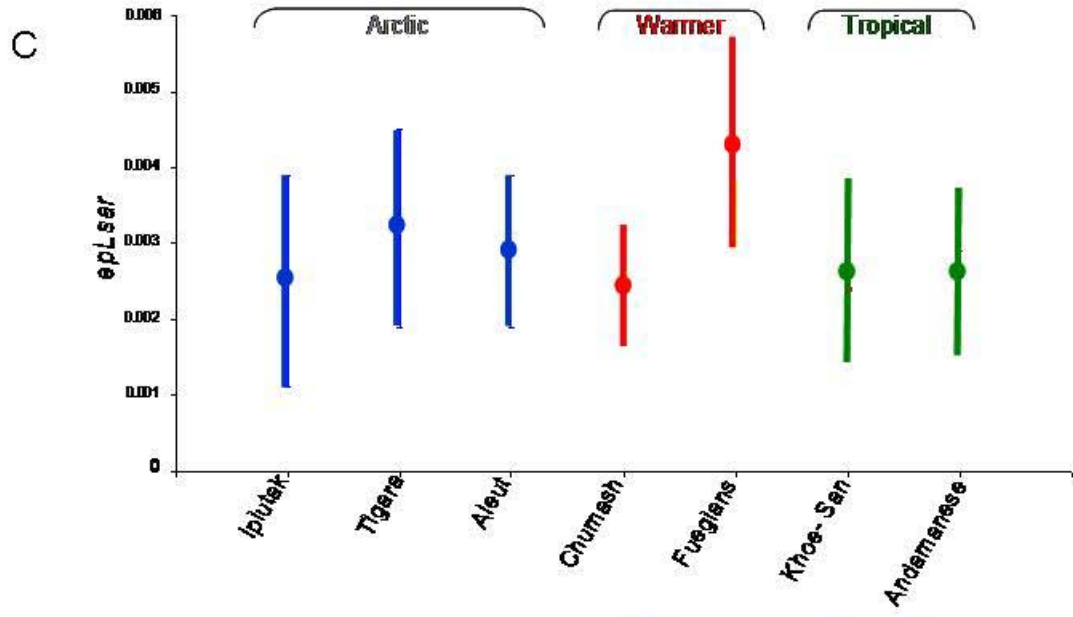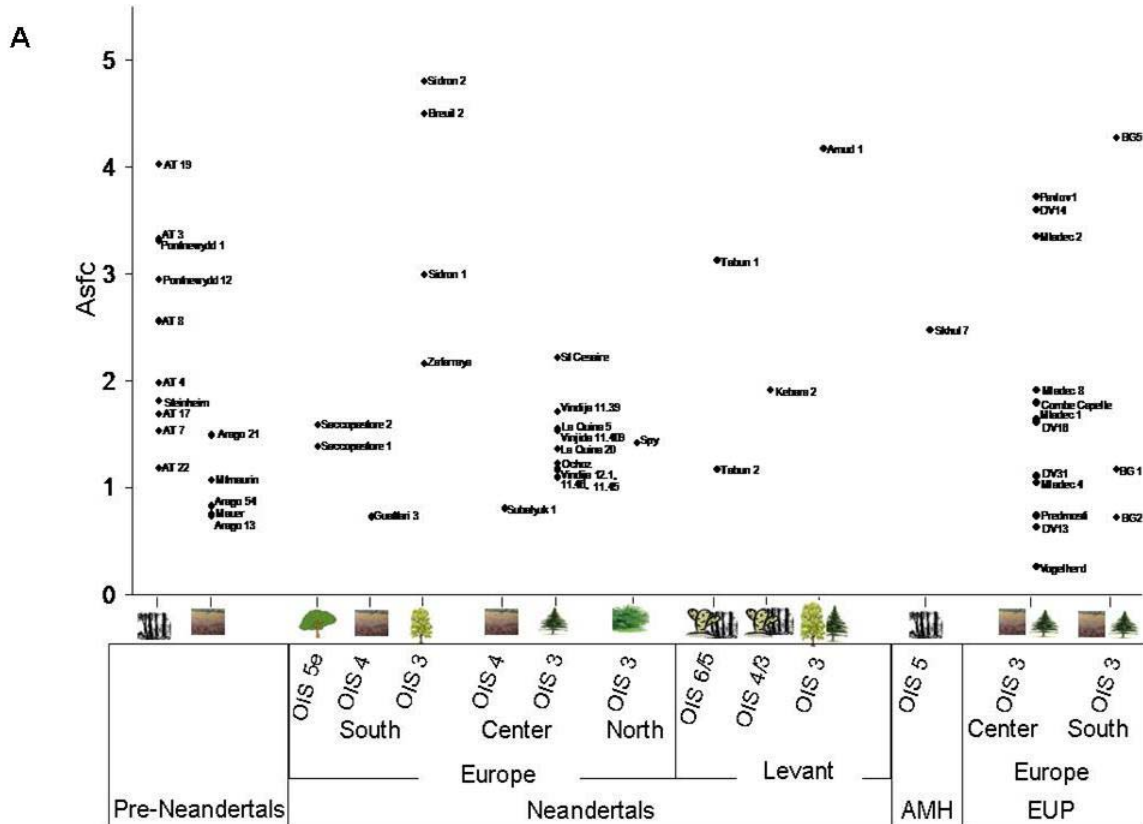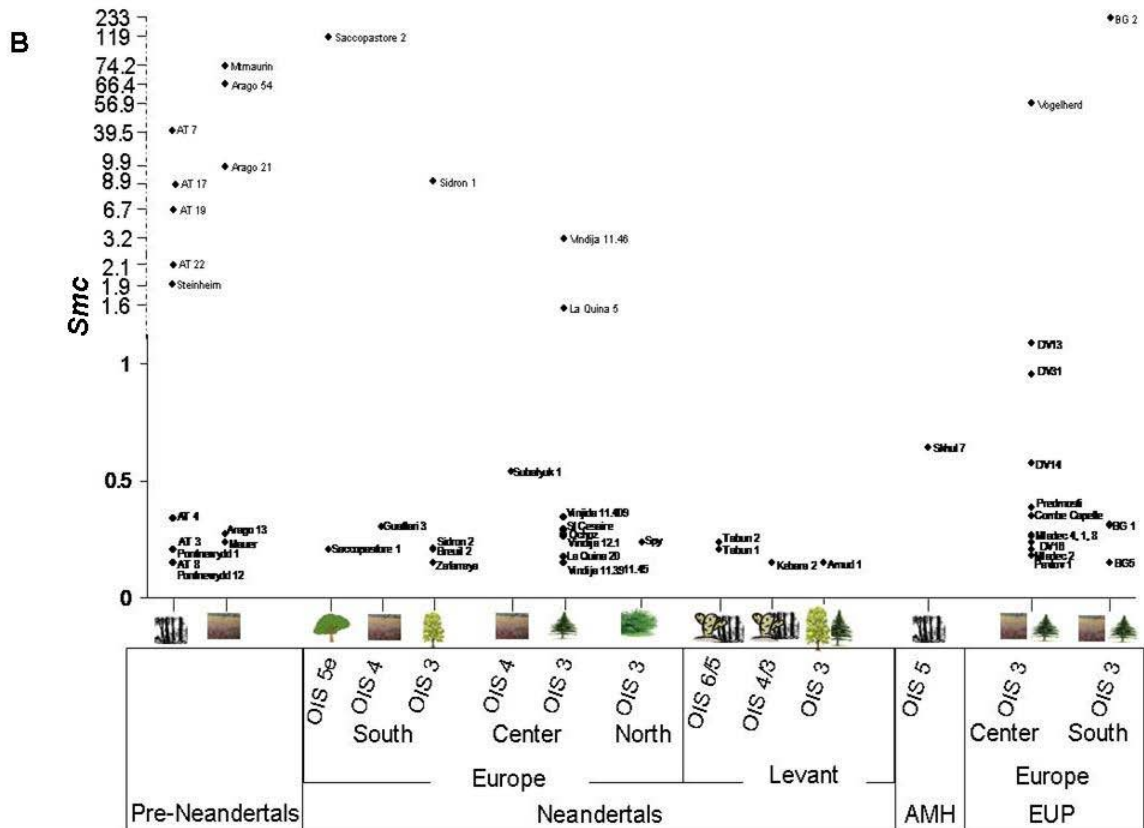
Figure 15. Individual plots for the fossil groups. A) *Asfc*, B) *Smc* and C) *epLsar*. Circles= sample means, horizontal lines = ±1 SD of the mean. Note that the Neandertal from Ochoz is placed with the Neandertals from central Europe dating to OIS 3. The stratigraphic position of this specimen is not certain and it was thus not included in the statistical analysis.
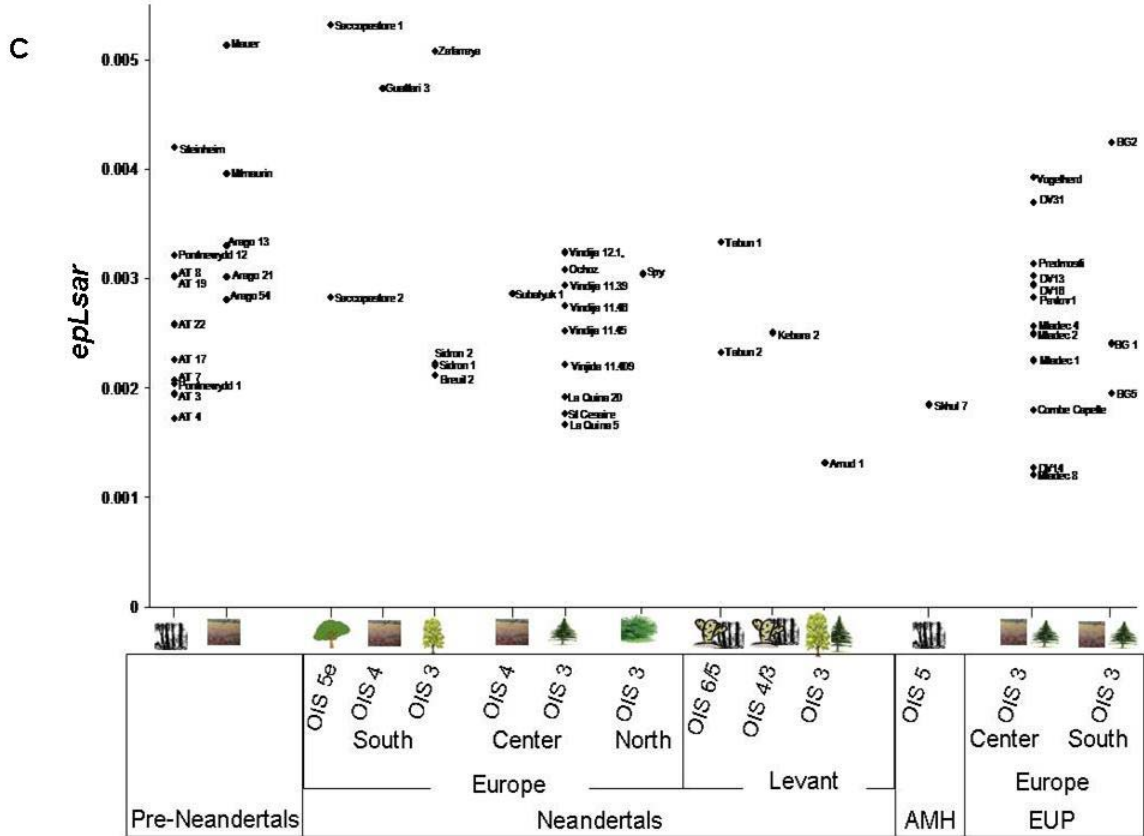
B

Chart showing Smc values across different hominin groups and time periods

c

epLsar

0.005

0.004

0.003

0.002

0.001

0

Mauer

Succopastore 1

Zafarraya

Guattari 3

Steinheim

Montmaurin

Arago 13

Pontnewydd 12

AT 8
AT 19

Arago 21

Arago 54

Vindija 12.1.

Ochoz

Spy

Tabun 1

Vogelherd

DV31

AT 22

Succopastore 2

Subalyuk 1

Vindija 11.39

Vindija 11.48

Predmosti

DV13

DV18

Pavlov1

Sidron 2

Vindija 11.45

Kebara 2

Mladec 4

Mladec 2

BG 1

AT 17

Sidron 1

Vinjija 11.409

Tabun 2

Mladec 1

AT 7

Pontnewydd 1

AT 3

Breuil 2

La Quina 20

St Cesaire

Skhul 7

Combe Capelle

BG5

AT 4

La Quina 5

Amud 1

DV14

Mladec 8

BG2

		OIS 5e	OIS 4	OIS 3	OIS 4	OIS 3	OIS 3	OIS 6/5	OIS 4/3	OIS 3	OIS 5	OIS 3	OIS 3
			South		Center		North		Levant			Center	South
				Europe					Levant			Europe	
Pre-Neandertals					Neandertals						AMH	EUP	

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Figure 16. Comparative statistics for the fossil groups. A) *Asfc*, B) *Smc* and C) *epLsar*.
Circles= sample means, horizontal lines = ±1 SD of the mean. Means and standard
deviations are not calculated for groups with less than three specimens. Note that the
Neandertal from Ochoz is placed with the Neandertals from central Europe dating to OIS
3. The stratigraphic position of this specimen is not certain and it was thus not included in
the statistical analysis.
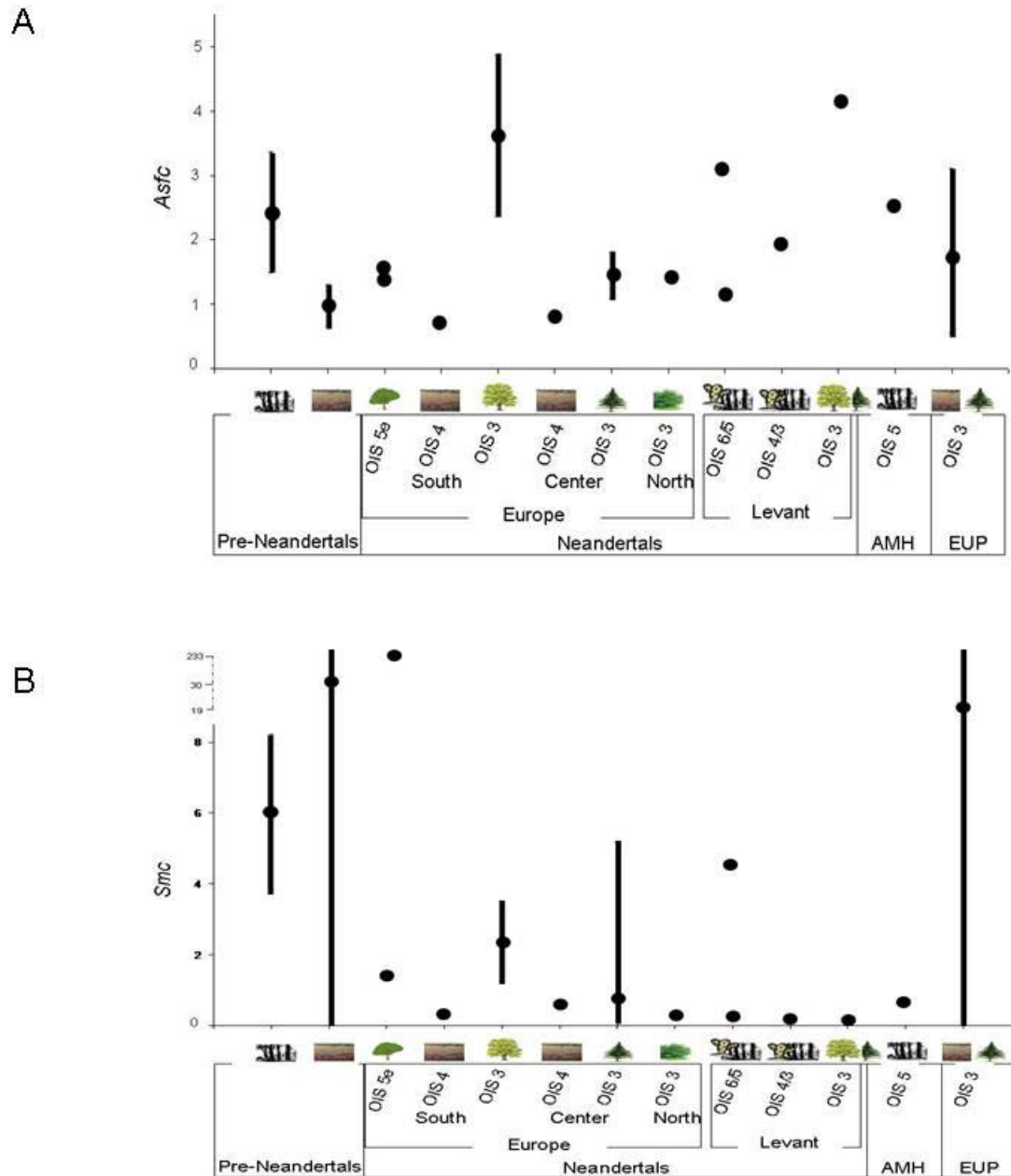
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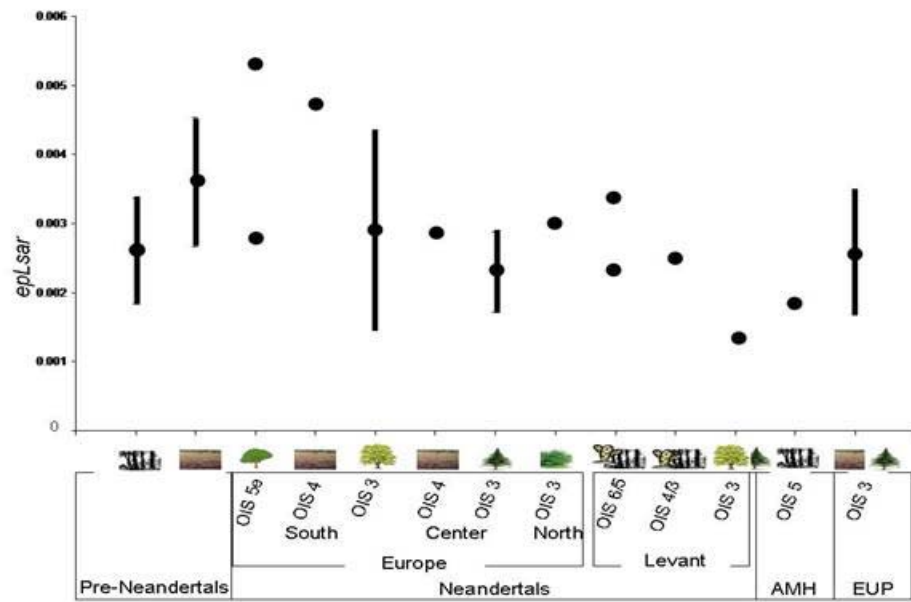
Figure 17. Comparative statistics for all modern and fossil groups analyzed in this study. A) *Asfc*, B) *Smc* and C) *epLsar*. Circles= sample means, horizontal lines = ±1 SD of the mean. Blue represents the carnivorous hunter-gatherers from arctic climates, green represents the mixed diet hunter-gatherers from the tropics, and red represents the carnivorous hunter-gatherers from warmer climates. All the fossil specimens are in black.
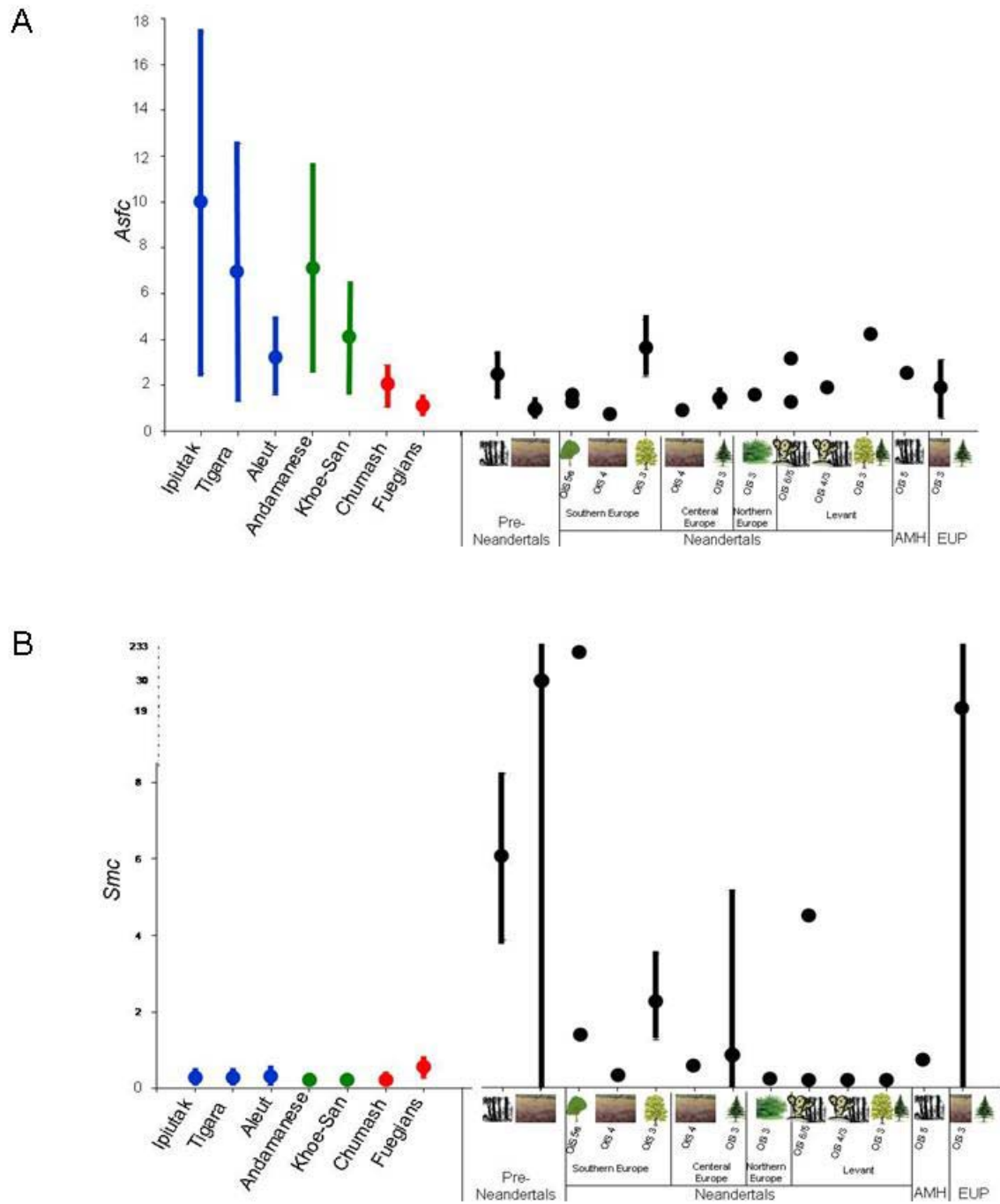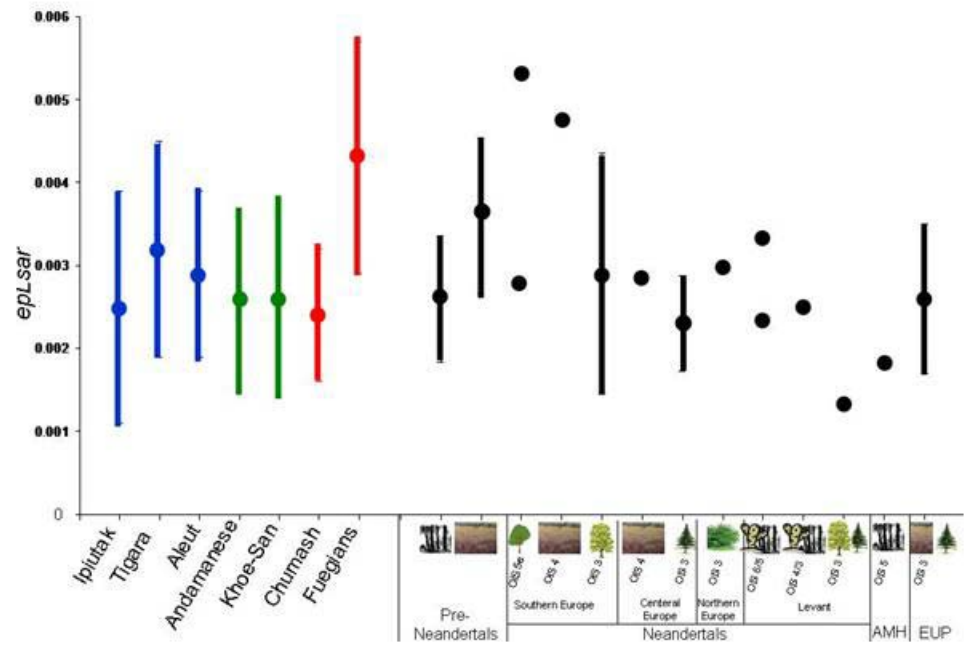
C

Figure 18. Results of a hierarchical cluster analysis using Euclidean distance and complete linkage for the fossil and recent sample. This cluster is for the complexity variable since it best illustrates the results of the post-hoc tests.
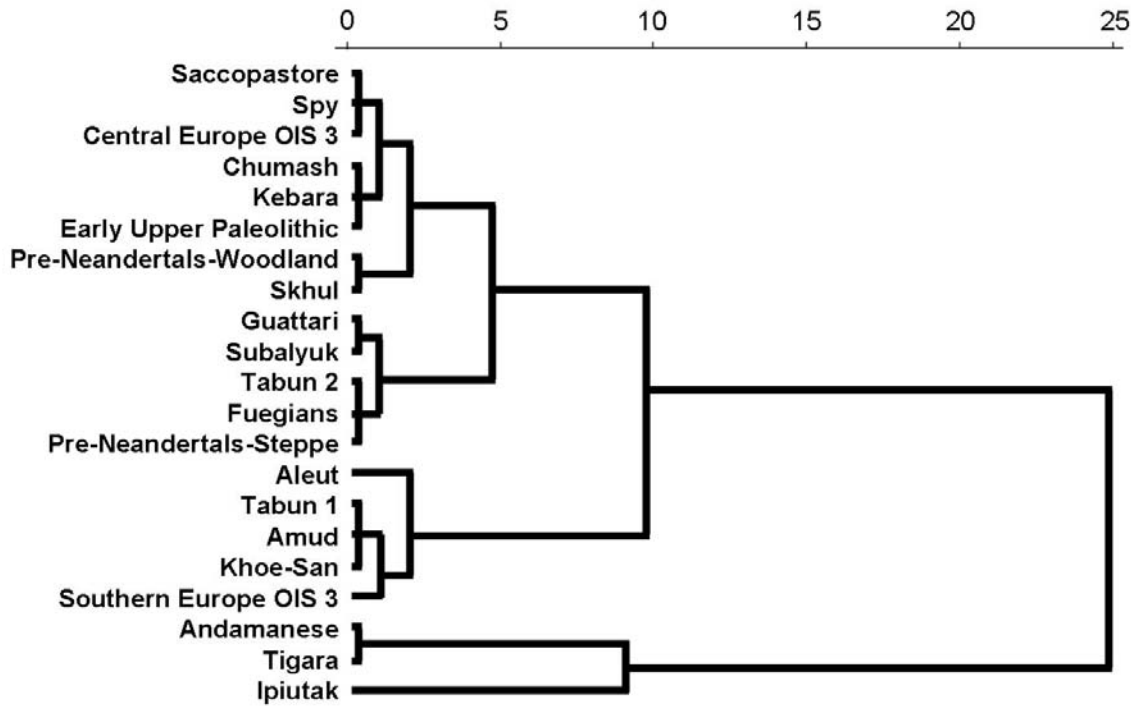
Figure 19. Modern sample means for *Asfc* and *Smc*. Diamonds represent ±1 SD of the mean. Blue represents the carnivorous hunter-gatherers from arctic climates, green represents the mixed diet hunter-gatherers from the tropics, and red represents the carnivorous hunter-gatherers from warmer climates.