Occlusal Wear Pattern Analysis of Functional Morphology in Neanderthals and Early *Homo sapiens* Dentition

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Summary

Very little is known about the occlusal wear pattern in the Neanderthal posterior dentition. Usually dental wear is closely related to the physical properties of the ingested food, and consequently can be used to obtain information about diet. Neanderthal dietary reconstructions have been mostly based on the analysis of accompanying faunal remains and isotopic signatures of bones and tooth enamel, suggesting that they exploited larger portions of animal proteins from large and medium-sized herbivores. Probably these studies may do not reflect the bulk diet, tending to underestimate plant consumption and to overestimate meat consumption.

In the present work the occlusal wear pattern of maxillary molars of *Homo neanderthalensis* (N=19) and early *Homo sapiens* (N=12)have been analyzed, applying non-destructive methods based on virtual three-dimensional polygonal models generated from surface scanning of dental casts. The sample groups occupied different geographical areas at different chronological times. The 3D digital tooth models were analyzed using the "Occlusal Fingerprint Analysis" (OFA) method (Kullmer et al. 2009), describing and quantifying the occlusal wear pattern derived from two wear facet angles (dip and dip direction), wear facet area and occlusal relief index (ORI). The OFA method provides information about the dynamics of the occlusal relationships and their function, permitting the reconstruction of the mandibular movements responsible for the contacts created during the chewing cycle. Since jaw movements and diet are closely related, the results obtained, can be used to interpret the diet of the two Pleistocene hominin species. In order to evaluate how dietary differences influence the occlusal wear pattern, upper molars of modern hunter-gatherers (N=42) with known diet and different dietary habits, have been included in the sample and compared with those of Neanderthals and early *Homo sapiens*.

Results show that within the modern hunter-gatherers sample, the occlusal wear pattern of carnivorous populations differs from those who relied on a mixed-diet. In particular, the study of relative facet areas clearly distinguish meat-eaters from mixed-diet hunter-gatherers, while ORI results and wear facet inclinations (dip angle) seem to reflect directly the abrasiveness of the diet, including the influence of exogenous materials during food preparation.

The Neanderthal occlusal wear pattern is characterized by an ecogeographic variation, suggesting the exploitation of different food resources. In particular Neanderthals who inhabited relatively warm environments of southern Europe and the Near East exhibit an occlusal wear pattern different from those of meat-eaters hunter-gatherers from tempered and cooler regions, displaying some features similar to those of Bushmen. These results suggest the exploitation of a broad variety of food sources. The analysis of the occlusal wear pattern in Neanderthals and early *Homo sapiens* who inhabited Europe during the cooler Oxygen Isotope Stage 3 (OIS3) shows many similarities between the two hominid species. These results indicate the exploitation of similar and low-diversified food sources, based mostly on the consumption of animal proteins, as suggested through the clear similarities with the wear patterns found in modern meat-eaters hunter-gatherers. In both studied groups, Neanderthals and early *Homo sapiens* the occlusal wear pattern is characterized by high ORI and dip angle values, suggesting the intake of a low-abrasive diet, probably due to the absence of sophisticated food preparation techniques introducing external silica grains, e.g. from soil (grinding of seeds) or plant cells, as those, seen in modern hunter-gatherer populations. The analysis of the occlusal fingerprints in Neanderthal and early European *Homo sapiens* upper molars suggests that both species followed very similar adaptive dietary strategies, based on a distinctive versatility and flexibility in the daily diet, depending on availability of resources according to environmental circumstances.

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Abbreviations

BP: Before Present

CVA: Canonical Variates Analysis

DEW: deciduous woodland

DWN: deciduous woodland Neanderthals

EHS: early *Homo sapiens*

HYP: hypocone

ISS: Immediate side shift

ka: kiloannum or one thousand years

LPT: lateroprotrusion

LRT: lateroretrusion

MDHG: mixed-diet hunter-gatherers

MED: Mediterranean evergreen

MEHG: meat-eaters hunter-gatherers

MEHS: Mediterranean evergreen early *Homo sapiens*

MEN: Mediterranean evergreen Neanderthals

MET: metacone

MHG: modern hunter-gatherers

MHS: modern *Homo sapiens*

MPHS: Middle Paleolithic *Homo sapiens*

MPT: medioprotrusion

MT: mediotrusion

NEA: Neanderthals

OFA: Occlusal Fingerprint Analysis

OIS: Oxygen Isotopic Stage

ORI: occlusal relief index

PAR: paracone

PRO: protocone

PT: protrusion

RT: retrusion

SCF: Steppe/Coniferous forest

SCN: Steppe/Coniferous forest Neanderthals

SEHS: Steppe/Coniferous forest early *Homo sapiens*

UPHS: Upper Paleolithic *Homo sapiens*

Chapter 1

The Neanderthals

1.1 General Overview

More than 150 years ago in 1856, partial human skeletal remains were discovered in the Feldhofer Cave along the Neander Valley (Mettmann, Germany), which were later attributed to a new human species, *Homo neanderthalensis* (King, 1864). Two other finds had already been made prior to 1856 - that of a juvenile skull at Engis in Belgium in 1830, and an adult skull at Forbes' Quarry in Gibraltar in 1848. Many years later, both fossils were recognized as Neanderthal specimens (Stringer & Gamble, 1993). The Neanderthal group was characterized by several distinctive anatomical features. For instance, the Neanderthal skull is elongated presenting a low forehead and a flat vault. The face shows prominent brow ridges, a large nasal cavity, and large and usually heavily worn frontal teeth. In the mandible the chin is absent (or weakly developed), and a retro-molar space behind the third molar is visible (Fig 1.1).

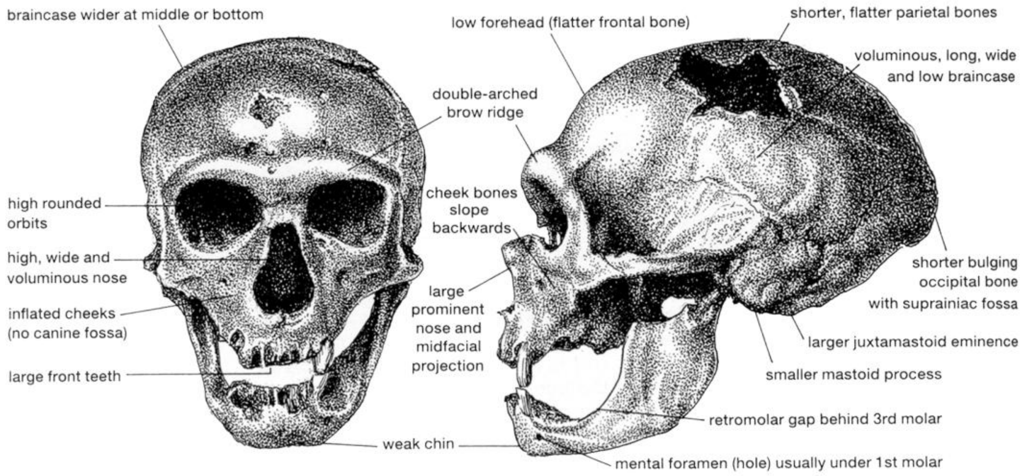


Figure A.1 - Neanderthal anatomical features in the Chapelle-aux-Saints skull (from Stringer & Gamble, 1993).

The postcranial skeleton presents a particular robustness, with short forearms and lower legs, and wide trunks. Many of the anatomical traits found in Neanderthals suggest an eco-geographical morphological adaptation to a cold climate (Coon, 1962; Trinkaus, 1981; Ruff, 1994; Holliday, 1997). The Pleistocene was characterized by repeated glacial and interglacial cycles. During the Neanderthal existence, western Eurasia was dominated by cool/temperate and glacial climates (Stringer & Gamble, 1993). The sea level decreased due to the expansion of the large ice sheet, which covered most parts of northern Europe and the British Isles during the coldest stage. The vegetation cover was reduced, with the formation of refuge woodlands along well-sheltered valleys, while the open environments were extended and characterized by strong aridity. The climate oscillations and rapid transition from one phase to another, led to strong selective pressure on the anatomy of European Neanderthal ancestors (Stringer & Gamble, 1993).

Figure 1.2 - The Neanderthal geographical range (modified from © 2009 Microsoft Corporation – Imagery © NASA). Ka = kiloannum or one thousand years.

The first Neanderthal features emerged in Europe during the Middle Pleistocene, becoming more evident through time, until the appearance of full Neanderthal morphology which characterized the "classic" Neanderthals, dated between 130 and 30 BP. Neanderthals colonized most of Western and Southern Europe, expanding into the Middle East. Recently, Neanderthal remains have been identified from caves in the Altai region of Siberia (Krause et al., 2007), extending the Neanderthal geographical range into central Asia (Fig. 1.2).

Neanderthal remains were most commonly found in association with a Mousterian industry, characterized by flakes and small hand axes detached from a prepared stone core. However, among some of the latest Neanderthal sites of Central and Western Europe, there have appeared some new technological features resembling those produced by early *Homo sapiens* (Harrold, 1989; Mellars, 2004; Delson & Harvati, 2006). Did they meet? Was the arrival of early *Homo sapiens* (EHS) in Europe a cause of Neanderthal extinction?

Neanderthals lived in Western Eurasia for more than 200,000 years, and disappeared during the last glacial period around 30 BP, after the colonization of Europe by EHS which took place around 40 BP. Therefore, there is an overlap of time of 8,000 to 10,000 years, where the two hominids species could have coexisted (Delson & Harvati, 2006), although recent radiocarbon dating shows that the speed of colonization of Europe by EHS populations was more rapid than previously believed, and that their period of coexistence with the preceding Neanderthals was shorter (Mellars, 2006). It has been proposed that the presence of variable Neanderthal anatomical traits found in some Upper Paleolithic EHS in Europe, are the product of a substantial degree of admixture between the two species (Trinkaus, 2007). Recent morphological studies (Harvati, 2002; Gunz & Harvati, 2007) and mitochondrial DNA analysis from Neanderthal and EHS remains (Serre et al., 2004; Currat & Excoffier, 2004) support a clear distinction between Neanderthals and EHS.

The rapid Neanderthal disappearance could reflect a direct competition for resources between the two species, where a more advanced technology and a more complex social organization could have favoured EHS (Mellars, 2004; Banks et al., 2008). It has also been proposed that the severe and unstable climate changes caused the fragmentation and degradation of the Neanderthal habitat, promoting weakness, isolation or extinction (Finlayson, 2000; Jiménez-Espejo et al., 2007). Since the Neanderthal populations had successfully adapted for more than 200,000 years surviving severe climatic fluctuations, it is more likely to hypothesize that the combination of elements such as environmental deterioration and intensified resource competition with EHS, led the Neanderthals to their extinction (Stringer et al., 2003).

1.2 Neanderthal Dental Morphology

The first descriptions of Neanderthal dentition focused on the particular morphology of anterior teeth. The upper incisors showed a shovel-like morphology, characterized by well developed lingual marginal ridges, marked lingual tubercles and a strong labial convexity

(Gorjanović-Kramberger, 1906; Crummett, 1994) (Fig.1.4). These morphological traits of the upper incisors can be found in different grades in other hominins also. If the high frequency and the combination of all three features are considered, it is possible to separate the Neanderthal group from EHS (Bailey, 2006).

The frontal teeth are large - significantly larger than those of modern humans (Brace, 1967; Wolpoff, 1971). It has been proposed that, the increased size found in the Neanderthal frontal teeth was caused by their extensive use as a third hand in processing material (Brace, 1967; Wolpoff, 1975).

An increase of the labio-lingual diameter in the frontal teeth would increase the resistance to the labio-lingually orientated forces (Trinkaus, 1978), suggesting a biomechanical response in the facial skeleton, causing a structural change of the facial topography (Rak, 1986; Trinkaus, 1987). Moreover, the large size of the Neanderthal anterior dentition could be related to allometric factors such as a reflection of large body sizes (Trinkaus, 1978). The lower incisors possess a simple morphology, similar to those of other hominids (Bailey, 2006). However, the lower incisors are distinctive in their relative size, being significantly larger than the posterior teeth compared to those of EHS (Stefan & Trinkaus, 1998). The upper canines are robust, convex lingually, and show a moderate degree of shovelling with high frequency of lingual tubercles and distal accessory ridges (Bailey, 2006). The lower canines tend to reflect the morphology of the upper canines, with no particular distinctive traits which can be used for taxonomy (Bailey, 2006).

Little attention has been paid in recent years to the morphology of the Neanderthal posterior dentition, considering it similar to the morphology seen in modern humans (e.g. Smith, 1976). Gorjanović-Kramberger (1908) noted an enlargement of the pulp cavity in the postcanine teeth at the expense of the roots in Neanderthal teeth from Krapina (Croatia) (Fig. 1.3). Subsequently Keith (1913) found this condition in other Neanderthal fossils and proposed the term ‘taurodontism’. Taurodontism has been considered a unique characteristic of the Neanderthals (e.g. Keith, 1913; Boule & Vallois, 1957; Hillson, 1986; Stringer & Gamble, 1993). However, this condition is highly variable in Neanderthals, and has also been found in some modern human populations (Blumberg et al., 1971). According to some scholars (Coon, 1962; Blumberg et al., 1971), taurodontism is an adaptation from an abrasive environment, with prolonging of the periodontium in populations with a high degree of wear.

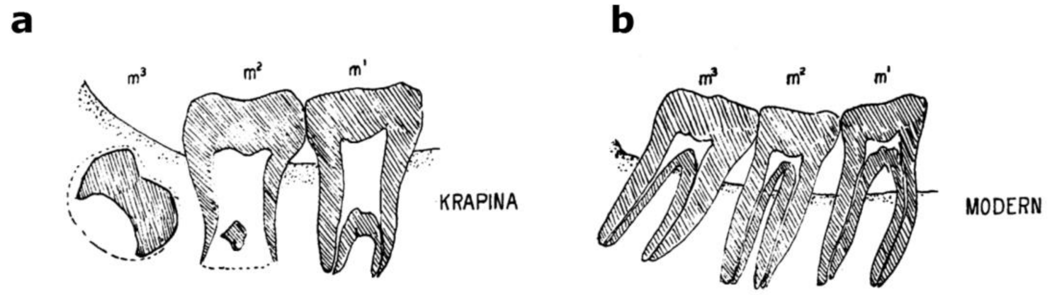


Figure 1.3 - Drawings of mid-sagittal sections of lower molars showing the enlargement of the pulp cavity in Neanderthals (a) and the absence of taurodontism in modern humans (b) (from Keith, 1913).

The traditional metric analysis of the postcanine dentition in Neanderthals and EHS has emphasized a large overlap between the two groups (Trinkaus, 1978; Manzi & Passarello, 1995). Recent studies have shown that Neanderthal tooth morphology of the posterior dentition is characterized by distinctive traits with a marked expression and high frequency, differing from those of EHS (Stringer et al., 1997; Bailey, 2002a, 2002b, 2004, 2006; Martinón-Torres et al., 2006; Gómez-Robles et al., 2007). The upper premolars in Neanderthals are characterized by a complex surface created by the presence of accessory crests and additional mesial and distal cusps, while in EHS the morphology is more simplified, especially in P^4 (Bailey, 2006). The mandibular premolars appeared to be more distinctive between Neanderthals and EHS. The Neanderthal P_3 shows an asymmetrical contour and a tooth surface characterized by the presence of a transverse crest connecting the buccal and the lingual cusps, while early modern human premolars display a simple morphology and a symmetrical outline (Bailey, 2006). The lower second premolars are characterized by a strong transverse crest, a well developed metaconid (Bailey, 2002b, 2006) displaced mesially (Martinón-Torres et al., 2006), and a marked asymmetrical crown (Bailey, 2002b, 2006; Martinón-Torres et al., 2006) (Fig. 1.4). The shape variation seen in the Neanderthal P_4s is produced by a combination of several factors, such as the restriction of the lingual portion (Bailey & Lynch, 2005), the broad occlusal polygon and the tooth size (Martinón-Torres et al., 2006).

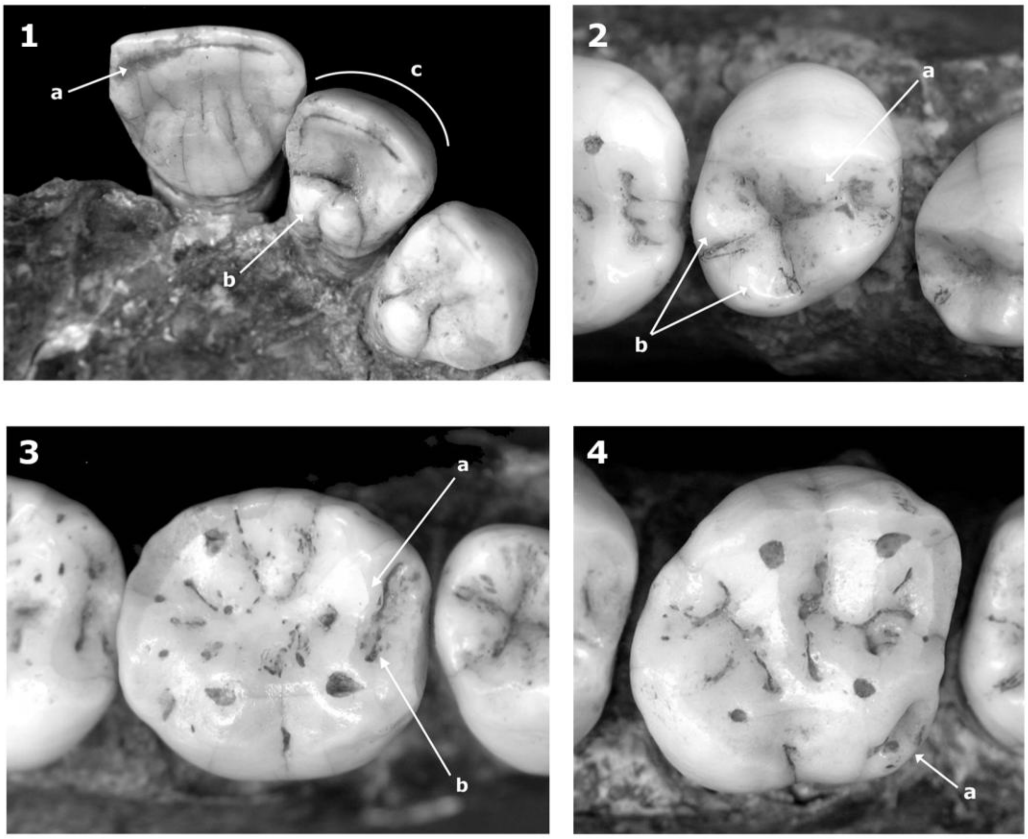


Figure 1.4 - Neanderthal tooth morphology. 1) Frontal teeth displaying the strong shoveling (a), the lingual tubercle (b) and labial convexity (c). 2) Lower P4 characterized by a marked transverse crest (a) and additional lingual cusps (b). 3) Lower M1 showing highlighted mid-trigonid crest (a) and anterior fovea (b). 4) Upper M1 with a marked Carabelli cusp (a). All the photos have been taken from the specimen of Le Moustier 1 housed at the Museum of Prehistory and Early History in Berlin.

In the maxillary molars, Neanderthals often exhibit a pattern where $M^2>M^1>M^3$, which differs significantly than those found in EHS, wherein exists a $M^1>M^2>M^3$ pattern (Trinkaus, 1978). The tooth crown of Neanderthal M^1s is commonly constituted by four cusps, characterized by a large hypocone which is never reduced or absent, a small metacone, and other additional accessory features (Bailey, 2002a, 2004, 2006). The Carabelli's trait is frequent and regularly well developed (Bailey, 2006) (Fig. 1.4). A distal fifth cusp, the hypoconule, is also common (Bailey, 2006). The occlusal morphology is characterized by a skewed contour and a rhomboidal shape, caused by the enlargement of the hypocone disto-lingually and by the disposition and configuration of the cusps which are internally compressed (Bailey, 2002a, 2004; Gómez-Robles et al., 2007). However this morphology is not unique to Neanderthals, and can also be found with less degree in early and middle Pleistocene European populations

(Gómez-Robles et al., 2007). Modern humans instead, show a reduced hypocone, a well developed metacone and a square occlusal polygon associated with a round external outline (Bailey, 2002a, 2004; Gómez-Robles et al., 2007).

The Neanderthal M^2 morphology, similarly to the upper M^1, is characterized by four well developed cusps, where the hypocone is rarely reduced and never absent (Bailey, 2002a, 2006). The additional cusps and accessory ridges in M^2 are less frequent than in M^1. However, the overall morphological traits do not differ significantly from the other hominid fossils and modern humans (Bailey, 2002a, 2002b). The M^3 of Neanderthals do not show particular differences to early and modern humans. The hypocone is often reduced or absent, Carabelli is scarcely present and rarely well developed, while accessory cusps derived from the mesial marginal ridge are still common (Bailey, 2006).

Neanderthals commonly show a mandibular molar pattern where M_3> M_2>M_1, while in modern humans M_1 is the largest, followed by M_2 and M_3 (Trinkaus, 1978). The most distinctive feature in Neanderthal lower molars is the presence of large anterior fovea bordered distally by a mid-trigonid crest (Bailey, 2002a, 2002b) (Fig. 1.4). The mid-trigonid crest is a low enameled and continuous ridge which connects the protoconid and the metaconid (Wu & Turner II, 1993), and was for the first time recognized by Vanderbroek (1967), and later described in Neanderthal fossils by Zubov (1992), who also noticed the absence of this crest in modern Europeans. Although in modern humans the metaconid and the protoconid can possess well developed crests, generally they do not join to form a continuous ridge (Bailey, 2002a, 2002b). In Neanderthals the mid-trigonid crest is almost always observed, with frequencies relatively constant in all three molars (Bailey, 2002a, 2002b). The presence of additional crests, fissures and cusps in Neanderthal M_1s reflects the complexity of the occlusal morphology. The Neanderthal M_1, characterized by a Y fissure pattern, never possesses less than five cusps, showing additional cusps such as C6 and C7 with moderate frequency (Bailey, 2006). The anterior fovea is often present, bordered distally by a continuous mid-trigonid crest (Bailey, 2002b, 2006). The Neanderthal M_2 shows a similar occlusal morphology seen in M_1, with a strong anterior fovea supported by a well developed mid-trigonid crest, a more frequent C6 and infrequent C7, maintaining five cusps and often a Y fissure pattern (Bailey, 2006). The relatively large size of Neanderthal M_3s(Trinkaus, 1978) determines the common presence of five or more cusps, higher than the adjacent molars, with a fissure pattern that could have a Y or X form, and a well developed mid-trigonid associated with a large anterior fovea (Bailey, 2006).

1.3 Neanderthal Tooth Wear

For many decades Neanderthal tooth wear has received little attention. Fraipont & Lohest (1887) noticed that the Spy fossils possessed heavy occlusal wear on the incisors. However, it was only in the 1960s that scientists focused on the anterior tooth wear of Neanderthals, explaining their functional and dietary relationships. Coon (1962) and Brace (1962, 1967) separately described the large anterior teeth of the Neanderthals and the heavy dental attrition, focusing especially on the occlusal wear pattern of the incisors.

Brace (1967) wrote:

"from the heavily rounded wear that characterizes Neanderthal incisors, it is evident that they were being used for more than just eating. It would seem that Neanderthal incisors were regularly used as a convenient all-purpose tool for cutting, tearing, holding and shaping a variety of objects"

Therefore, according to Coon and Brace, the heavily rounded wear of the Neanderthal incisors was mostly due to paramasticatory uses. However, Wallace (1975) in analysing the frontal teeth of La Ferrassie I found some similarities in the Bushmen anterior dentition and suggested that the rounded incisors were caused by contact with abrasives in the diet. Subsequently, the analysis of buccal striations (Bermúdez de Castro et al., 1988), the microwear studies of labial scratches in the anterior dentition (Lalueza Fox & Frayer, 1997; Lozano et al., 2008), and the rate of bevelling of the incisors (Ungar et al., 1997), confirmed that Neanderthals used their frontal teeth as a tool, holding pieces of meat or other material between their frontal teeth. Moreover the high degree of wear found in Neanderthal frontal teeth is attributed to an anterior edge-to-edge occlusion (Wallace, 1975; Kaifu et al., 2003), where the frontal teeth of upper and lower jaws meet along their incisal edges during maximum intercuspation (or centric occlusion).

Many of the Neanderthal specimens show heavy interproximal wear, especially marked between adjacent premolars and molars (Trinkaus, 1983) (Fig. 1.5). Interproximal tooth wear is the result of tooth-to-tooth contact and crown movements occurring during the chewing cycle.

Figure 1.5 - Interproximal wear in Neanderthal dentition: interproximal wear facet (a) and artificial groove caused by toothpicking (b). Photos of Neanderthals specimens (Krapina 10 and Krapina 60) uploaded from NESPOS website.

Two main forces are involved during masticatory movements: a lateral force that directs bucco-lingually and a mesial force vector that pushes the teeth to migrate anteriorly (Picton, 1962). Wolpoff (1971) argued that the foremost factor implicated in the mesial migration is due to the mesial root angulation of the teeth and the direction of the jaw movements during mastication. Some authors (e.g., Kaidonis et al.,1992; Villa and Giacobini, 1996) observed the presence of vertical furrows on the interproximal wear facets in Australian aboriginal dentitions, introducing the possibility that vertical movements may also be involved in producing interproximal wear. Moreover, interproximal wear in selected human groups is related to the magnitude of the masticatory forces due to diet and food preparation (Hinton, 1982). The interproximal attrition rate is age-related and increases with advanced age (Kieser et al., 1985). As the complexity of these movements creates a strong correlation in size, morphology, orientation and angulation between contiguous interproximal wear facets, these facets have increasingly been used for tooth and specimen association in Neanderthal samples (Wolpoff, 1978, 1979; Radovčić et al., 1988; Coppa et al., 2005). Many evidences have been documented in hominid fossils and in many human populations, wherein interproximal tooth wear can also be created by the use of teeth as a tool for task activity (Brown & Molnar, 1990), or by the use of toothpicking for dental hygiene (Frayer & Russel, 1987; Lukacs and Pastor, 1988; Ungar et al., 2001; Hlusko, 2003; Agger et al., 2004; Molnar, 2008). Frayer & Russel (1987) reported on the presence of artificial grooves along the cementum-enamel junction in several Neanderthal Krapina specimens (Fig. 1.5). Since these artificial grooves resemble those present in recent populations which have been attributed to toothpick use, Frayel & Russell argued that Neanderthals were habitually cleaning the interproximal dental space with a toothpick.

Very little is known about the occlusal wear in the Neanderthal posterior dentition. Occlusal wear was generally used for age determination (e.g. Wolpoff, 1979). Advanced degree of occlusal wear was associated with abrasive food or an abrasive environment (Trinkaus, 1983). In recent years scientists have focused on the analysis of occlusal and buccal microwear of Neanderthal posterior dentition in order to reconstruct their diet. Patterns of dental microwear such as the proportion and orientation of vertical and horizontal striations, the relation between scratches and pits or the tooth surface textures, reflect the physical properties of foods eaten (Gordon, 1986; Lalueza et al., 1996; Pérez-Pérez et al., 2003; El Zaatari S., 2007a, 2007b; Ungar et al., 2008). However, no information exists in the literature regarding the occlusal macro-wear pattern in Neanderthal molars - the difference in occlusal macro-wear between Neanderthals from different geographical areas, different time periods or from different climate conditions. How does the occlusal macro-wear in Neanderthals change in relation to diet? How does the different tooth morphology seen in Neanderthals affect the occlusal macro-wear pattern?

1.4 Neanderthal Diet

The reconstruction of the ecology of Neanderthals such as foraging strategies, subsistence and land-use, is mainly based on the study of associated faunal assemblages and stone tool technology (e.g. Patou-Matis, 2000; Burke, 2004; Hockett & Haws, 2005). The great abundance of animal remains found in Neanderthal sites suggests a diet rich in meat (e.g. Patou-Matis, 2000). This evidence is also supported by the analysis of the frequency and pattern of cut-marks found on the animal bones, which indicate butchery and defleshing (Noe-Nygaard, 1977; Patou-Matis, 2000). Moreover, the high degree of bone fractures and burnt bones point out that Neanderthals also consumed the bone marrow, extracting it via boiling methods (Patou-Matis, 1995).

For many years it was debated whether Neanderthals were active hunters or scavengers (e.g. Stringer & Gamble, 1993). The subsistence strategies documented are characterized by variability, including evidence of both hunting and scavenging (Stiner, 1994; Burke, 2004). The study of the mortality profile of the faunal assemblage highlights the preponderance of young and old individuals, which demonstrates that Neanderthals selectively hunted, choosing their prey based on age and size (Speth & Tchernov, 2001; Burke, 2004; Steele, 2004; Rabinovich & Hovers, 2000).

In central and northern Europe Neanderthals relied mostly on large herbivores living in open environments such as horse, bison and reindeer, preferentially hunting two or three species or specializing on a single species (Patou-Matis, 2000). The degree of specialized hunting seems more frequent during temperate or cold phases (Patou-Mathis, 2000). At lower latitudes such as south-western France and northern Spain, the Neanderthal subsistence shows low prey diversity but differs from those of northern Neanderthals. In addition to the open environment herbivores, the lower latitude Neanderthals also exploited woodland habitats focusing mainly on medium-sized herbivores such as red deer, ibex, wild boar, roe deer and chamois (Boyle, 2000; Hockett & Haws, 2005). In the Mediterranean area, the Neanderthal diet featured large and medium-sized terrestrial mammals (Aura Tortosa et al., 2002). However, along the Mediterranean coastlines there is evidence suggesting consumption of other food sources (Hockett & Haws, 2005). Shellfish exploitation has been reported in several Mousterian caves in Italy and Gibraltar (Stiner, 1994; Barton, 2000; Finlayson et al., 2006; Stringer et al., 2008). The faunal assemblage of the Mousterian Grotta dei Moscerini (Italy) was mainly composed of small animals, including insectivores, lagomorphs, rodents, tortoises, marine and terrestrial molluscs and even marine sponges (Stiner, 1994). Vanguard Cave (Gibraltar) also provides evidence of marine food supply, such as molluscs, seals, dolphins and fish (Stringer et al., 2008). The Gibraltar and Italian examples indicate that mussels and other shellfish probably contributed regularly to the Neanderthal diet (Stiner, 1994; Barton, 2000).

In the Near East the faunal remains primarily consisted of gazelle, fallow deer, red deer, wild boar and aurochs (Speth & Tchernov, 1998, 2001).

Recently, stable carbon and nitrogen isotopic signatures of collagen from Neanderthal bones have been widely used for palaeodietary reconstruction (Fizet et al., 1995; Bocherens et al., 1999, 2001, 2005; Richards et al., 2000; Drucker & Bocherens, 2004; Beauval et al., 2006). The collagen synthesized during the life of the bone tissues reflects the average dietary proteic fraction in the form of isotopic signatures (Bocherens et al., 2001). The measurement of the ratio of the stable isotopes of carbon allow to identify the type of plants at the base of the trophic pyramid, while with the study of nitrogen stable isotopes it is possible to recognize the position of a specimen within the food trophic pyramid (Bocherens et al., 2001). This method has been applied to thirteen adult Neanderthals from three sites in France, two sites in Belgium and one site in Croatia (Richards et al., 2008). All these studies support the hypothesis built on the analysis of the faunal remains, pointing out that Neanderthals obtained nearly all of their dietary proteins from animal sources, occupying the higher level of the food trophic web, similarly to the top-level carnivores of these sites. Neanderthals were active hunters, preferring large herbivores from open environments. The protein from plants shows they were an insignificant part of the Neanderthal diet (Richards et al., 2000). The Neanderthals of Saint-Césaire consumed the meat of very large species such as woolly rhinoceros and especially woolly mammoth (Bocherens et al., 2005). Recently, the use of stable isotopes for palaeodietary reconstruction has also been applied to collagen extracted from the tooth dentin of the Neanderthals from the site of Jonzac (Richards et al., 2008). The isotopic data from the dentin tissue probably does not reflect the lifetime average as bones do, but rather a specific period of time of formation such as the diet at the ages of later childhood/early adolescence (Richards et al., 2008).

Similar results where Neanderthals seemed to have a diet rich in animal proteins is also confirmed by the analysis of buccal microwear from the molar teeth of modern hunter-gatherers and Pleistocene hominids (Lalueza et al., 1996). The pattern of buccal microwear such as the orientation of the striations, striation density and ratio between scratches and pits reflects dietary habits including information regarding food processing (Pérez-Pérez et al., 1994). The modern hunter-gatherers – relying mostly on animal sources – such as the Inuit, Indians from Vancouver Island, Lapps and Fuegians, show a low number of striations with a high frequency of vertical striations (Lalueza et al., 1996). In contrast hunter-gatherers with mixed-diet such as Bushmen, Australian aborigines, Tasmanian and Andamanese islanders display a large number of striations dominated by horizontal striations (Lalueza et al., 1996). The high number of striations could reflect the presence of plant phytoliths in the diet (Chiocon et al., 1990), and be responsible for the presence of scratches in a highly vegetarian diet (Lalueza et al., 1996). The high frequency of vertical striations in the carnivorous hunter-gatherers could be caused by the predominance of vertical mandibular movements, while the mastication of hard and fibrous materials, such as vegetables, may need more horizontal movements (Hinton, 1981, 1982; Lalueza et al., 1996). The relative frequency of striations might be indicative of the nature of the diet and of the preponderance of plant and meat food, while the absolute number of striations would be a reflection of the general abrasiveness of the diet (Lalueza et al., 1996). The Neanderthal buccal microwear is similar to those of the carnivorous hunter-gatherers, indicating a diet which included mostly meat (Lalueza et al., 1996). However Neanderthal specimens from Marillac, Saint-Césaire and Malarnaud show a similar pattern to those of the mixed-diet hunter-gatherers, suggesting a geographical and temporal variability within the Neanderthal group (Lalueza et al., 1996).

Although a few studies indicate that EHS were also active hunters focusing mainly on the consumption of meat from terrestrial herbivores (Drucker & Bocherens, 2004; Stewart, 2004), the analysis of faunal assemblages, lithic industry and stable isotopic studies suggest that EHS had a broader dietary spectrum than Neanderthals (Stiner, 1994; Svoboda et al., 2000; Bosinski, 2000; Hahn, 2000; Pérles, 2000; Richards et al., 2001; Hockett & Haws, 2005). In the Czech Republic, the Upper Paleolithic site of Pavlov reveals that nearly 10% of the faunal remains was constituted by birds, while in Dolni Vestonice the discovery of grinding stone tools probably suggests the exploitation of plant foods (Svoboda et al., 2000). Numerous Upper Paleolithic sites in Germany contain fish remains (Bosinski, 2000; Hahn, 2000). In southern Greece, data from Franchthi Cave shows evidence of fish, shellfish, plants and bird exploitation (Pérles, 2000). The carbon and nitrogen stable isotope values from European EHS remains of upper and middle Paleolithic indicate a diet based on significant use of freshwater aquatic resources, such as fish, molluscs and birds (Richards et al., 2001).

In summary, Neanderthals from central and northern Europe had a low-diversity diet, consisting mostly of meat and organs from two or three large herbivore species, rich in fat and high in energy, which was probably an advantage in cold climates where the thermoregulation of the body requires higher energy intakes (Stini, 1981), while the southern Neanderthals from Mediterranean coastlines had a more diversified diet enriched by the exploitation of small animals and marine shellfish (Hockett & Haws, 2005). However, such a restricted diet of the northern and middle latitude Neanderthals lacks essential nutrients, and could have increased the maternal and fetal-to-infant mortality rates and decreased life expectancy (Hockett & Haws, 2005). This hypothesis is also confirmed by the paleopathological patterns found in Neanderthals which pointed out a low life-expectancy where 70-80% of the individuals died before the age of 40, and also showed an increase of dental hypoplasias indicating periods of poor nutrition and/or starvation (Trinkaus, 1995). Indeed, along the Mediterranean coastlines, where the climate fluctuations were less severe, there was the possibility of isolated glacial refuges capable of providing greater and variable food sources which enriched the diet of the Neanderthals, prolonging their survival, which is also confirmed by the new dating from Gorham's cave in Gibraltar (Finlayson et al., 2006).

The first EHS populations that arrived in Europe were characterized by small groups, geographically dispersed and distributed along rivers and coastlines (Davies, 2001; Burke, 2004). This pattern of distribution combined with a broader dietary spectrum could have reduced the possible competition between Neanderthal and EHS leading to an initial period of ecological equilibrium (Burke, 2004). However, in the long run, the more diversified diet of EHS brought to a demographic expansion which caused an increased competitive relationship with Neanderthals (Burke, 2004; Hockett & Haws, 2005). The demographic expansion of EHS combined with a more advanced stone tool technology could have been one of the causes which led to Neanderthal extinction (Burke, 2004; Hockett & Haws, 2005).

Although the analysis of faunal remains, stable isotopes of tooth and bone collagen, and buccal microwear in Neanderthals highlights a diet consisting almost solely of animal proteins, new evidence suggests that the Neanderthals could have exploited broader and more diverse food sources.

Boule & Vallois (1957) in analysing the Neanderthal specimen of La Ferrassie, hypothesized a consumption of a herbivorous diet due to the presence of a shallow structure of the temporomandibular joint, which could permit a greater lateral motion of the mandible.

The cave deposits in Amud (Israel) contain numerous plant fossils, some of them edible, suggesting that a broad spectrum of plants had been exploited by Neanderthals from the end of Middle Paleolithic (Madella et al., 2002). Also in the Kebara Cave (Israel) the Neanderthal remains are associated with a large collection of seeds and plants, mostly composed by legumes, pistachios and acorns (Albert et al., 2000; Lev et al., 2005). The studies of Speth & Tchernov (2001) indicate that Neanderthals occupied the Kebara Cave during winter and early spring focusing mostly on the hunting of gazelles and fallow deer, as well as in late spring and summer.

Therefore the animal sources overlap with the spring legumes and the fall nuts and acorns, increasing and widening the dietary breadth of the Kebara Neanderthals (Lev et al., 2005).

Moreover, the study of microfossil plants trapped in the dental calculus of Shanidar III, a Neanderthal fossil from northern Iraq, represents the first direct evidence of the inclusion of plant material, such as starch grain from grasses, in the Neanderthal diet (Henry & Piperno, 2008).

A further analysis of buccal microwear shows differences in density and orientation of the striations indicating that Middle Pleistocene humans had a more abrasive diet than late Pleistocene populations (Pérez-Pérez et al., 2003). In addition the Neanderthal group is characterized by a heterogeneous microwear pattern, probably caused by the exploitation of different food sources (Pérez-Pérez et al., 2003). The different microwear patterns found in Neanderthals seem to reflect the climate fluctuations rather than geographical dispersal (Pérez-Pérez et al., 2003). The Neanderthal specimens that lived during the warm periods show fewer striations than those of colder stages, indicating the possible addition of abrasive foodstuffs such as roots or bulbs in the diet, during colder periods (Pérez-Pérez et al., 2003). Moreover, a recent study of occlusal microwear texture confirms a variable dietary spectrum for Neanderthals, and suggests an eco-geographic variation (El Zaatari, 2007a, 2007b). In the northern latitudes where the vegetation was constituted by steppe and tundra, Neanderthals appeared to be similar to the modern hunter-gatherers relying mostly on meat like Fuegians, whereas those Neanderthals from forested environments resemble the Chumash who inhabited Mediterranean-like areas (El Zaatari, 2007a, 2007b). Neanderthals from the deciduous forests of southern Europe, instead show a microwear pattern close to those of mixed-diet hunter-gatherers (El Zaatari, 2007a, 2007b). Finally, the microscopic examination of stone tools found at the Mousterian site of La Quina in France, showed evidence of plant processing, suggesting the exploitation of a variety of plant types (Hardy, 2004). Although the deposits accumulated at the La Quina site indicate an open environment characterized by cold and dry steppe conditions, the presence of the Voultron river near the site may have provided a microhabitat more conducive to plant life (Hardy, 2004).

The Neanderthals occupied a variety of different geographical areas (from Europe to the Near East), at different chronological times, facing different climatic conditions, which determined the presence of different environments. New evidence supports the idea that Neanderthals living in different environments may have exploited different food sources.

Chapter 2

Function, Morphology and Wear of Teeth during Occlusion

2.1 Occlusion

Dental occlusion is the contact between opposing maxillary and mandibular teeth during jaw closure. Full occlusion (or centric occlusion) is attained in the maximal intercuspation position, referred as the best fit of the teeth regardless of the condylar position (Glossary of Prosthodontic terms, 2005). The extent of occlusal contact affects electric muscle activity, bite force, jaw movements and masticatory efficiency (Bakke, 1993). A better masticatory efficiency is obtained through occlusal stability (Bakke, 1993), defined as the equalization of contacts that prevents tooth movement after closure (Glossary of Prosthodontic terms, 2005). Therefore, in order to resist vertical and horizontal forces, the occlusal surface of opposing teeth tends to be intercuspated (Douglas & DeVreugd, 1997). The incisal edges of the upper anterior teeth overlap mesially with the incisal edges of the opposing lower anterior teeth and the main cusp of the maxillary canine occludes between the buccal surface of the lower canine and first premolar (Hillson, 2003). The buccal cusps of the mandibular molars and premolars occlude with the fossae of the opposing maxillary cheek teeth, while the lingual cusps of the upper posterior teeth are in contact with the corresponding fossae of the lower cheek teeth (Hillson, 2003).

In dentistry the natural dentition is divided into two main occlusal configurations (Douglas & DeVreugd, 1997): the group function occlusion has multiple contact relations between the maxillary and mandibular teeth in lateral movements on the working side whereby simultaneous contact of several teeth acts as a group to distribute occlusal forces. Anterior guidance (or mutually protected occlusion) is an occlusal scheme in which the anterior teeth disengage the posterior teeth in all mandibular excursive movements, and the posterior teeth prevent excessive contact of the anterior teeth in maximum intercuspation (Glossary of

Prosthodontic terms, 2005). The occlusal forces during the intercuspation position are best directed along the long axes of teeth (Ramfjord & Ash, 1971; Jordan & Abrams, 1992; Okeson, 1993). The cusps of the posterior dentition can act as vertical stops to jaw closure (functional or support cusps) or as cutting edges during mastication (guiding cusps) (Douglas & DeVreugd, 1997). The support cusps are positioned near the center of the root diameter, distributing the occlusal forces directly over the root (Douglas & DeVreugd, 1997). In the posterior dentition an apparent reversed occlusal relationship occurs where the support cusps opposing the vertical load of the first premolars are best positioned on the mandibular teeth, while in the molars the lingual cusps of the maxillary teeth are better positioned (Douglas & DeVreugd, 1997).

The occlusal surface shows varying degrees of inclination and defines a curved occlusal plane (Hillson, 2003) (Fig. 2.1). The Curve of Spee (1890) positions the long axes of the teeth along the path of mandibular closure in anteroposterior direction (Douglas & DeVreugd, 1997). The Curve of Wilson (1911) is a translated curve produced by the lingual inclination of the mandibular posterior teeth, where the lower arch appears to be concave and the upper arch convex (Douglas & DeVreugd, 1997; Glossary of Prosthodontic terms, 2005). The Sphere of Monson (1922), similar to the Curve of Wilson, describes the plane of the molars with the lower occlusal surfaces inclined to lingual and the upper inclined to buccal (Hillson, 2003).
The helicoidal plane is the change in slope of the occlusal surface from mesial to distal along the tooth row (Smith, 1986). In order to generate the helicoidal plane, many hypotheses have been proposed. With the advancement of the degree of wear acting mainly on the supporting cusps (lingually in the upper molars and buccally in the lowers), the ideal Curve of Monson changes into a flat plane, and then into a Reversed Curve (Osborne, 1982). According to Smith (1986) the helicoidal plane is also the result of the axial inclination, where third molars are more inclined than the second, followed by the first. Moreover, Macho & Berner (1994) found that the enamel of the first molar was thinner than the second and third molars, which would accelerate the tendency of the first molar to reverse the Curve of Monson. It is probable that the helicoidal plane is a combination of a variety of factors (Hillson, 2003).
Any deviation from a normal occlusion is considered as malocclusion (Glossary of Prosthodontic terms, 2005).

The first identification of the type of malocclusions present in the modern human dentition date back to 1899 with Angle's Classification, which is defined by the position of the paracone of the first molar in relation to the lower first molar (Hillson, 2003) (Fig. 2.2).

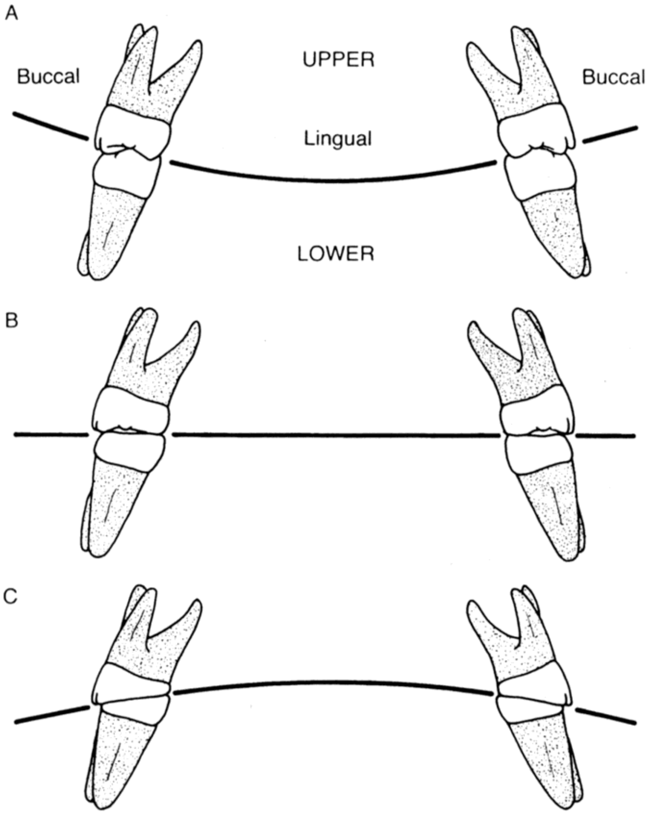


Figure 2.1 - Development of the helicoidal plane of attrition: a) curve of Monson, b) flat occlusal plane with moderate wear and c) Reversed Curve of Monson with advanced wear (from Hillson, 2003).

Angle recognized four types of malocclusions (Glossary of Prosthodontic terms, 2005):

Class I (normal occlusion or neutrocclusion): the dental relationship in which there is a normal anteroposterior relationship of the jaws, as indicated by correct interdigitation of maxillary and mandibular molars, where the paracone occludes with the buccal groove of the lower molar.

Class II (distocclusion): the dental relationship in which the mandibular dental arch is posterior to the maxillary dental arch in one or both lateral segments; the mandibular first molar is distal to the maxillary first molar. Class II can be further subdivided into two divisions.
Division 1: bilateral distal retrusion with a narrow maxillary arch and protruding maxillary incisors.

Division 2: bilateral distal with a normal or square-shaped maxillary arch, retruded maxillary central incisors, labially malposed maxillary lateral incisors, and an excessive vertical overlap.

Class III (mesiocclusion): the dental relationship in which the mandibular arch is anterior to the maxillary arch in one or both lateral segments; the mandibular first molar is mesial to the maxillary first molar. The mandibular incisors are usually in anterior cross bite.

Class IV: the dental relationship in which the occlusal relations of the dental arches present the peculiar condition of being in distal occlusion in one lateral half and in mesial occlusion in the other (no longer used).

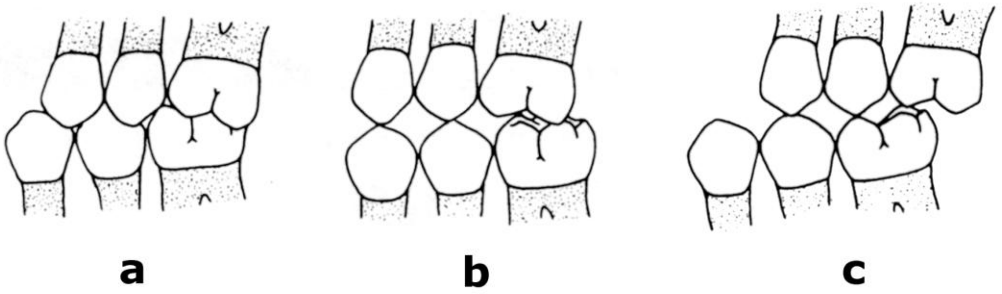


Figure 2.2 - Major types of malocclusion based on the Angle's classification: a) Angle Class I, b) Angle Class II and c) Angle Class III (modified from Hillson, 2003).

The anterior dentition are also characterized by different types of occlusion , which are classified based on the vertical and horizontal overlap between maxillary and mandibular opposing teeth, called overjet and overbite respectively (Fig. 2.3).

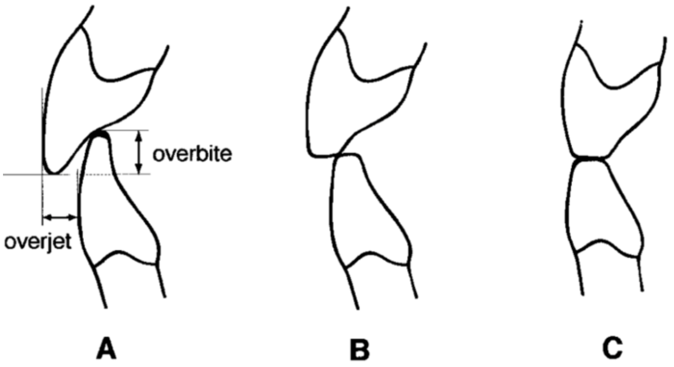


Figure 2.3 - Anterior occlusion. a) Scissor occlusion where overbite > 0 and overjet > 0; b) intermediate condition where overbite = 0 and overjet > 0; c) edge-to-edge occlusion where overbite = 0 and overjet = 0 (from Kaifu et al., 2003).

A large part of dentistry has often considered the static textbook normal occlusion definition as a physiologically, functionally and anatomically correct occlusion in *Homo sapiens*. However, Begg (1954) proposed the concept of attritional occlusion, where occlusion equates to a dynamic process, changing continuously due to attritional tooth reduction and the compensatory physiological tooth migration that occurs throughout life. Begg (1954) built his hypothesis on the study of the dentition of pre-European-contact Australian aborigines, characterized by a hunter-gatherer subsistence based on a tough and fibrous diet. He concluded that after eruption the frontal teeth showed a scissors occlusion, while the posterior dentition was characterized by rapid occlusal and interproximal wear. The continuous pressure of the mesial drift, higher in the lower teeth, combined with rapid occlusal wear, caused the modification of the anterior occlusion in adults which showed an edge-to-edge occlusion. Moreover, Begg (1954) noted that the dentition of the Australian aborigines showed a low incidence of dental irregularity and dental diseases which commonly affect modern and industrialized society, suggesting that a correct occlusion could be attained only when the dentition is subjected to sufficient attritional pressure. Although the arguments of Begg (1954) did not consider populations other than Australian aborigines, and are based on untested observations lacking quantitative documentation, many points of his hypothesis show strong evidence (Kaifu et al., 2003). The human dentition evolved in heavy-wear environments until relatively recently. Some dental problems in contemporary societies appear to reflect the disparity between the original design of our dentition and our present environment, in which extensive wear no longer occurs (Kaifu et al., 2003).

2.2 The Chewing Cycle

Mammals are characterized by a heterodont dentition with complex cheek teeth (dyphyodont type) especially evolved for chewing, grinding and cutting, and by the possession of a superficial masseter muscle which makes the lateral movements of the mandible possible (Janis, 1990; Campbell, 1998). Mammals need to maintain a high metabolic rate and therefore need constant nourishing. The evolution of a new type of dentition associated with a new kind of jaw function allowed a more complete and effective exploitation of the environment's resources (Campbell, 1998). During mastication the food is broken down and reduced to small pieces, providing an increased surface area for the digestive enzymes to act upon. Thus mammals were able to exploit food resources that were not available to their reptilian predecessors (Campbell, 1998).

All mammals chew on one side of the jaw at a time, and move the lower jaw in an orbital circuit (Janis, 1990). The masticatory cycle of mammals begins with puncture-crushing (Crompton & Hiiemae, 1970; Hiiemae & Crompton, 1971; Hiiemae & Kay, 1972; Kay & Hiiemae, 1974; Hiiemae 1978) characterized primarily by vertical mandibular movements where the food is pulped and tooth-to-tooth contact rarely occurs. During puncture-crushing the dental wear is characterized by coarse surfaces and blunt cusp tips, produced by the contact with food and any foreign materials included, such as grit or sand (abrasion) (Stone, 1948; Hiiemae & Kay, 1973; Kay, 1977). After the food has initially been reduced and softened by puncture-crushing, a rhythmic chewing phase (or power stroke) follows where the jaw movements are guided by the occlusal morphology of the upper and lower teeth (Crompton & Hiiemae, 1970; Kay & Hiiemae, 1974). The contacts between crests, cusps and basins of upper and lower dentition produce the formation of attritional wear areas characterized by a smooth, polished and well delineated surface (wear facet). During the chewing phase the food undergoes three main masticatory processes (Kay & Hiiemae, 1974) (Fig. 2.4):

Shearing is the force which causes the sliding of opposing parts of the teeth in a direction almost parallel to their planes of contact.

Crushing is the force distributed between two hard bodies in a direction nearly perpendicular to the contact plane.

Grinding is the resulting action of the combination of perpendicular and parallel forces to the contact plane.

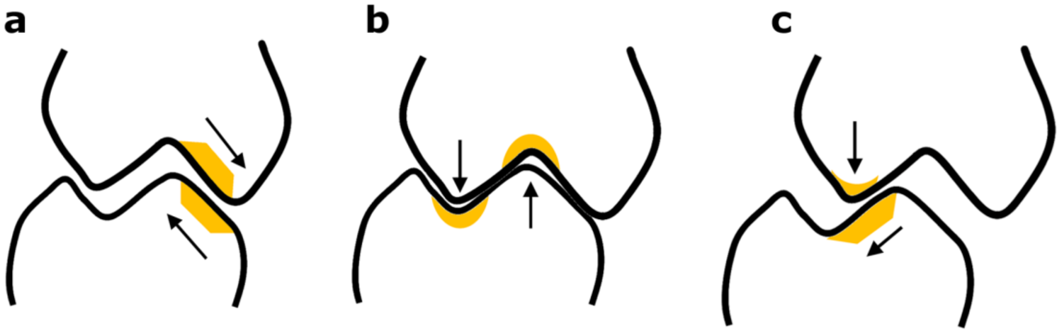


Figure 2.4 - Masticatory processes during the chewing phase: a) shearing, b) crushing and c) grinding.

The power stroke is divided in two phases (Hiiemae & Kay, 1972; Hiiemae & Kay, 1973; Kay & Hiiemae, 1974) (Fig. 2.5). During the first part of the power stroke (Phase I), the opposing molar crests tend to slide past each other and the trapped food is exposed to a shearing action. At the end of Phase I, food is compressed (crushing) between basins and cusps of molars which are moving to result in centric occlusion. Phase II is an anterior-medial movement, where the lower molars move out of occlusion. During Phase II food is processed by grinding through the contact between the lingual slopes of the mandibular molar cusps and the buccal surfaces of the maxillary molar cusps, which act as a "pestle and mortar". The chewing cycle terminates with the jaw opening.

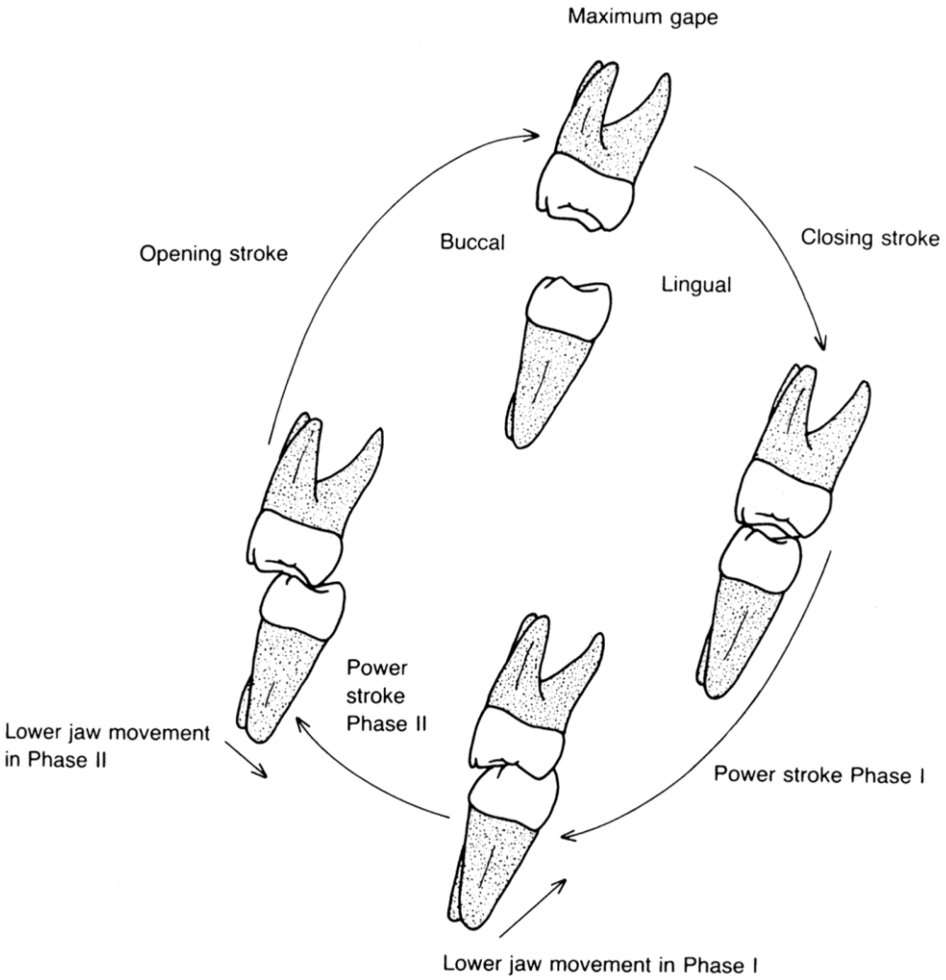


Figure 2.5 - The chewing cycle (from Hillson, 2003).

The angle of ascent of the lower jaw, and the extent of the medial component of the movement, is largely dependent on the diet of the animal (Janis, 1990). In general, the chewing cycle of carnivores is mainly constituted by puncture-crushing movements, characterized by steep vertical movement of the lower jaw, while herbivores have a chewing cycle composed almost entirely of rhythmic chewing with a preponderance of horizontal mandibular movements (Crompton & Hiiemae, 1969; Hiiemae, 1978). The human masticatory movements vary, depending on genetic and environmental factors, and also on the occlusal relationships (Douglas & DeVreugd, 1997). In Angle's Class II Division II the masticatory movements are more vertical, while in an Angle's Class II with anterior edge-to-edge relationships the jaw movements are mainly horizontal (Bakke, 1993).

2.3 Occlusal Tooth Wear

Tooth wear is the gradual loss of tooth surface caused by three processes: attrition, abrasion and erosion.

Attrition: is the mechanical wear produced by tooth-to-tooth contact without the presence of food, between adjacent and opposing teeth producing flat and shiny areas with well-defined borders called wear facets (Every, 1972; Kaidonis et al., 1993; Imfeld, 1996; Hillson, 2003; Glossary of Prosthodontic terms, 2005; Kaidonis, 2008). The surface of the wear facets are covered with minute sub-parallel striations mirroring the orientation of tooth movements (Kay, 1977). Every facet is matched by a corresponding facet on a tooth in the opposing arch, and when dentin is exposed it remains flat with no "scooping" (Kaidonis, 2008). Wear facets are generally created by contact during normal mastication (Mills 1963, 1967; Wolpoff 1971; Butler, 1981). However, wear facets can be also produced by other non-masticatory activities such as bruxism, which is an oral habit consisting of involuntary rhythmic or spasmodic, non-functional gnashing, grinding, or clenching of teeth (Glossary of Prosthodontic terms, 2005). Bruxism generates far greater forces than those applied during chewing (Hillson, 2003). Many scientists have attempted to diagnose bruxism using a visual examination of the wear facets (Graf, 1969; Lindqvist, 1974; Negoro et al., 1998; Restrepo et al., 2006). Graf (1969) suggested that the wear facets created by bruxism show a shiny surface with sharp edges. Lindqvist (1974) proposed that bruxism could be recognized by the presence of atypical wear facets, characterized by flat smooth areas that correspond with similar opposing areas when the mandible has moved at least 3-5 mm from centric occlusion in a lateral excursion. However, often these visual approaches did not consider clearly the difference between pathological and physiological wear (Restrepo et al., 2006). Pathological dental wear is often localized on the guiding or cutting cusps of the posterior dentition, on the cusps of the canine and along the incisors (Australian & Levi, 1966). Moreover, the dental plane produced by bruxism is characterized by a plane surface that sometimes reaches the dentin, surrounded by enamel zones (Mehl et al., 1997). Restrepo et al. (2006) in considering the differentiation between normal and pathological wear, has shown that the irregular movements of the mandible during non-masticatory function produce irregular forms of dental wear in the bruxist group.

Abrasion: is the friction of exogenous materials forced over tooth surfaces (Kaifu et al., 2003; Kaidonis, 2008). The abrasive particles are usually contained in the food, however other foreign objects can also cause abrasion such as dust present in the environment, or tools used for oral hygiene such as toothbrush and toothpaste (Addy & Shellis, 2006). The action of food on a tooth surface is not anatomically specific; it does not create distinct and localized wear facets rather occurring over the whole occlusal surface (Kaidonis, 2008). Most abrasion does not produce characteristic features, progressively reducing the sharpness of microscopic details on the tooth crown and the information regarding the orientation of the tooth movements (Scott et al., 1949; Kay, 1977; Hillson, 2003). However, the abrasive action of food on the tooth surface generates particular microwear patterns characterized by pits and striations that if studied under microscope reveal the type of diet consumed or foreign bodies forced over the tooth surface (Every, 1972; Kaisonis, 2008). Dentin exposures caused by abrasion in contrast with the attritional wear, illustrate scooping (Kaidonis, 2008).

In hunter-gatherer populations, especially those from desert environments, abrasion represents the most prevalent mechanism of wear, caused mainly by the mastication of tough and fibrous materials (Barrett, 1977; Kaidonis, 2008). In contrast with hunter-gatherer subsistence, abrasion in modern and industrialized society is due to tooth brushing using abrasive toothpaste, which creates smooth surfaces with high gloss (Hillson, 2003; Addy & Shellis, 2006).

Erosion: is the loss of tooth structure due to chemical dissolution without the involvement of bacteria (Kaifu et al., 2003; Addy & Shellis, 2006; Kaidonis, 2008). Erosion produces defects that are sharply defined, wedge-shaped depressions often in facial and cervical areas (Glossary of Prosthodontic terms, 2005). Although dentinal scooping is commonly associated with erosion, the eroded occlusal surface displays significant differences in shape compared with that caused mainly by abrasion (Bell et al., 1998). Chemical dissolution could be created by different types of acids, intrinsic (regurgitated gastric acids), and extrinsic (soft drinks, pickles and acidic fruits) (Addy & Shellis, 2006). Enamel exposed to acid loses minerals from the superficial layer (softening) (Koulourides, 1968). With time, as softening progresses further into the enamel, dissolution in the outermost enamel layer will reach the point where this layer of enamel is lost completely (Schweizer-Hirt et al., 1978; Eisenburger et al., 2000; Addy & Shellis, 2006).

The study of skeletal remains of hunter-gatherers and historic and prehistoric European populations, showed no evidence of dental erosion (Aubry et al., 2003; Aaron, 2004). Although early hunter-gatherer populations could introduce acids into their diet through the consumption of acidic fruits or berries, this intake was seasonal and would not show particular erosive effects on the tooth surface (Kaidonis, 2008). Moreover, saliva would have played a significant protective role as did the presence of biofilms as physical barriers (Kaidonis, 2008). In contrast with earlier populations, erosion seems to be a dental pathology which affects western society, mainly caused by the high consumption of erosive drinks (Addy & Shellis, 2006; Kaidonis, 2008).

The mechanisms of attrition, abrasion and erosion act together, each with a varying intensity and duration to produce a multitude of different wear patterns (Kaidonis, 2008). For example, the direct removal of hard tissue by complete dissolution creates a thin softened layer, which becomes vulnerable to subsequent mechanical wear (Featherstone & Lussi, 2006). Although the types of wear are generally characterized by distinct patterns, it is difficult in many cases to either determine the major cause of wear or to evaluate how different wear mechanisms have interacted (Addy & Shellis, 2006).

2.4 Physical Properties of Food

The physical properties of the ingested food may be the primary factors affecting changes in dental morphology (Strait, 1997). Shapes of teeth are designed to answer functional demands necessary to breakdown foods having various physical properties (Lucas, 1979, 1980; Luke & Lucas, 1983; Lucas & Luke, 1984; Lucas & Teaford, 1994).

Different terms have been widely used regarding the structure, texture and consistency of food items. Here we present some of the most common terms used, based on the glossary created by Jowitt (1974). The terms *hard*, *tough*, *soft*, *tender* and *brittle*, are terms relating to the behaviour of the material under stress or strain. *Gritty* and *coarse* are terms related to the particle size or shape, while *fibrous* is a term related to shape and arrangement of structural elements.

Hard: possessing the textural property manifested by a high resistance to deformation by applied force.

Tough: possessing the textural property manifested by a high and persistent resistance to breakdown on mastication.

Soft: possessing the textural property manifested by a low resistance to deformation by applied force.

Tender: possessing the textural property manifested by a low resistance to breakdown on mastication.

Brittle: possessing the textural property manifested by a tendency to crack, fracture or shatter without substantial prior deformation on the application of force.

Gritty: possessing the textural property manifested by the presence of small hard particles.

Coarse: possessing the textural property manifested by large constituent particles.

Fibrous: possessing the textural property manifested by the presence predominantly of readily-separated filamentous structural elements.

2.5 Occlusal Wear Facets

The occlusal wear facet is the product of tooth-to-tooth attritional contact during the chewing phase. A wear facet is characterized by a smooth and polished enameled area with well-defined borders. Since the structures of the masticatory apparatus involved in the chewing cycle of mammals and the morphology of teeth are considered homologous, the resulting wear facets can also be considered homologous (Janis, 1990). Butler (1952) showed for the first time that wear facets of different species were homologous, and proposed a labeling system for their identification. Over the years, different studies have adopted different labeling systems, creating conflicts and confusion (Tab. 2.1). Butler (1952, 1973) (Fig. 2.6a) and Mills (1955) analyzed the teeth of primates and perissodactyla identifying ten main facets. Crompton and Hiiemae (1970) recognized six wear facets on the molars of the American opossum.

Crompton (1971) described the wear pattern on early mammals also identifying six facets but with a different labeling system.

Table 2.1 - Occlusal wear facet labeling system used by various authors (modified from Kay, 1977).

Butler (1952, 1973) Mills (1955)	Crompton & Hiiemae 1970	Crompton 1971	Gingerich 1974	Kay & Hiiemae 1974	Kay 1977	Maier 1977	Maier & Schneck 1981
1	1	2a/b	B2	2a/b	2a/b	2	2
2	2	1a/b	B1	1a/b	1a/b	1	1
3	4	5	B5	5	5	5	5
4, 4'				8	8	8	8
5			L2	10	10n	10,12	10,12
6	3	3a/b	B3	3a/b	3a/b	3	3
7	6	4a/b	B4	4a/b	4a/b	4	4, 4'
8,8'			B7	7	7n	7	7
9	5	6	B6	6	6	6	6
10			L1	9	9, x	9, 11	9, 11 13

Subsequently Gingerich (1974) proposed a new numbering system based on the molars of the Paleocene primate Plesiadapis, identifying nine wear facets. Kay & Hiiemae (1974) – based on the work of Crompton (1971) – divided the wear facets by referencing the phases of the powerstroke of mastication, recognizing ten facets on the molars of primates, eight phase I facets (1 to 8) and two phase II facets (9 and 10). Kay (1977) subsequently modified the numbering system and added one more phase II facet (x) (Fig. 2.6c and d).

In the same year Maier (1977) analyzed the bilophodont molars of Cercopithecoids based on the work of Kay & Hiimeae (1974) including two additional pairs of facets belonging to phase II (11 and 12) (Fig. 2.6b). Later, Maier & Schneck (1981) in analyzing the hominoid molars added one more pair of wear facets to phase II areas (13) (Fig. 2.6f).

Although the facets of the lower molars are the product of contact with one single facet of the corresponding upper molars, occasionally lower molar facets come into contact with two upper molar facets. The position of the contacts between facets is determined by the morphological variation of the occlusal relationship known as Angle's Class (Ulhaas et al., 2007).

The following description of wear facets on molars is based on the works of Maier & Schneck (1981) (Fig. 2.6f). The dental nomenclature is primarily based on the works of Van Valen (1968), Szalay (1968, 1969) and Kay (1977). *Phase I facets.* Wear facet 1 on the upper molars develops along the mesio-lingual slope of the paracone, between the praeparacrista and the entoparacrista. The corresponding facet 1 of the lower molar is located buccally to the postprotocristid. Facet 2 of the upper molars forms on the metacone, lingual to the postmetacrista and distal to the entometacrista. The matching wear facet 2 is found on the mesio-buccal slope of the protoconid developing along the praeprotocristid.

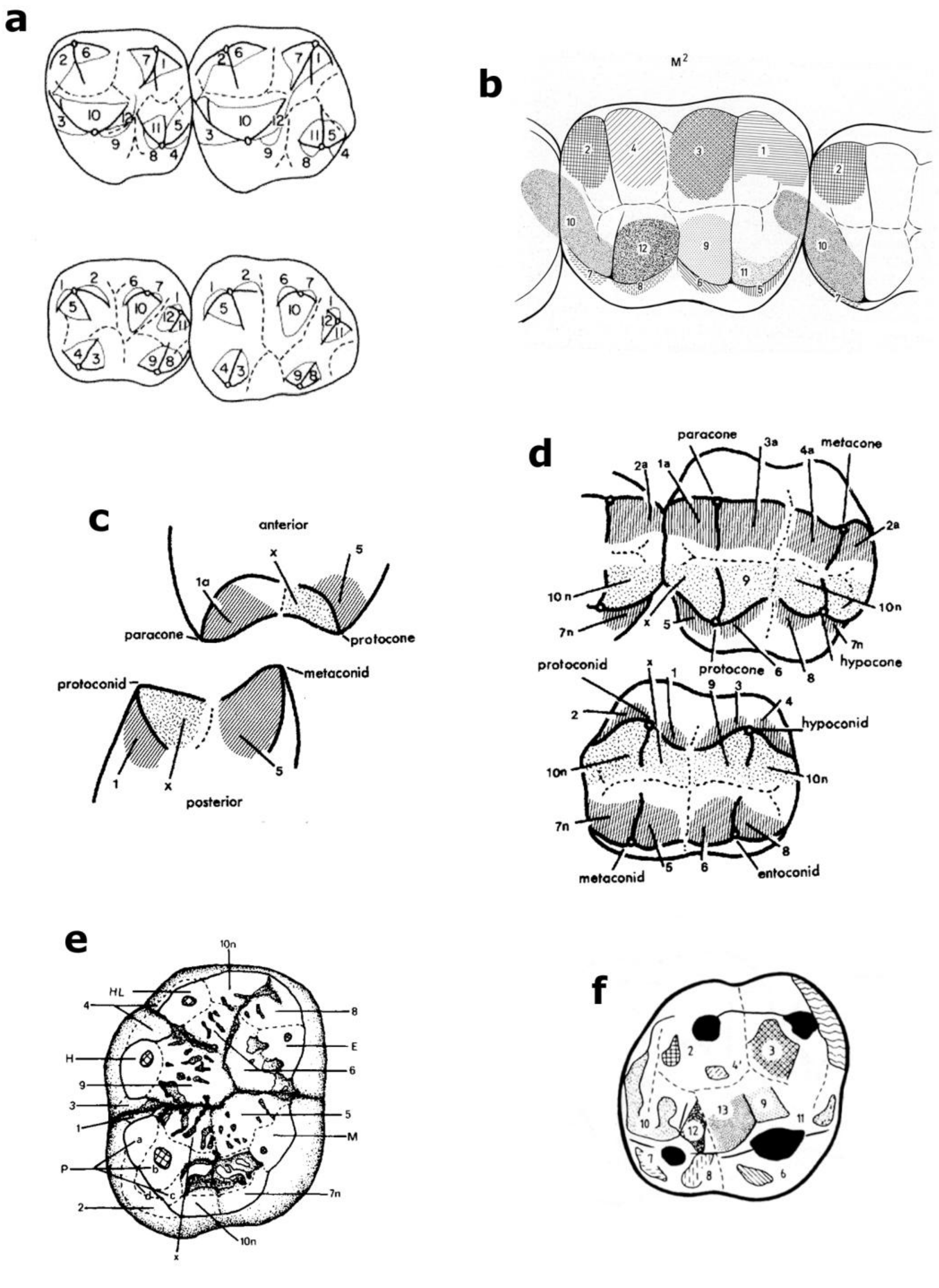


Figure 2.6 - Occlusal wear facet numbering system. Butler, 1977 (a); Maier, 1977 (b); Kay, 1977 (c and d); Gordon, 1984 (e); Maier and Schneck, 1981 (f).

In the upper molars, facet 3 is found between the postparacrista and the entoparacrista. The corresponding facet is developed buccally to the praehypocristid in the lower molars. Facet 4 of the maxillary molars is located on the mesio-lingual slope of the metacone, between the praemetacrista and the entometacrista. On the mandibular molars, facet 4 forms buccally along the posthypocristid. On the lingual side of the upper molars, facet 5 develops lingually to the praeprotocrista, while the matching facet is located in the metaconid area situated between the ectometacristid and the postmetacristid. Facet 6 is formed on the disto-lingual slope of the protocone, along the postprotocrista. The corresponding lower facet is located between the ectoentocristid and the praeentocristid. Facet 7 of the upper molars develops distally to the posthypocrista in the hypocone area. In the lower molars facet 7 is located between the ectometacristid and the praemetacristid. On the mesio-lingual slope of the hypocone, facet 8 forms along the praehypocrista. The corresponding occlusal area is found in the entoconid area formed along the ectoentocristid and the postentocristid.

Phase II facets. The wear facet 9 is formed on the maxillary molars on the buccal slope of the protocone between the praeprotocrista and the ectoprotocrista. The matching wear area is located on the lingual slope of the hypoconid, lingual to the praehypocristid and posthypocristid. Facet 10 develops in the hypocone area situated between the posthypocrista and the ectohypocrista. On the lower molars, facet 10 is found on the mesio-lingual slope of the protoconid, formed between the praeprotocristid and the entoprotocristid. In the upper molars, along the anterior fovea area, facet 11 forms distally to the praeprotocrista. The matching area is located between the postprotocristid and the entoprotocristid of the lower molars. Wear facet 12 develops on the mesio-buccal slope of the hypocone in the upper molars between the praehypocrista and the ectohypocrista. The correspondent facet in the lower molars is located distally to the entohypoconulidcristid. Wear facet 13 forms in the upper molars along the disto-buccal slope of the protocone, between the ectoprotocrista and the postprotocrista. The matching facet is developed mesially to the entohypoconulidcristid.

In summation, the buccal phase I facets (1 to 4) are formed along the slopes of the paracone and the metacone in the upper molars, and on the slopes of the protoconid and hypoconid in the lowers. The lingual phase I facets (5 to 8) are localized on the slopes of the protocone and hypocone of the maxillary molars, and on the slopes of the hypoconulid and entoconid in the lower molars. The phase II facets (9 to 13) develop along the buccal slopes of the protocone and hypocone in the upper molars, and along the lingual slope of the hypoconid, protoconid and hypoconulid in the lower molars. At the beginning of phase I of the powerstroke, both buccal and lingual facets of upper and lower molars are involved in the shearing action on the food bolus. At the end of phase I, the food bolus is compressed by a crushing action between basins and cusps approaching the maximum intercuspation. During phase II of the chewing cycle the food bolus is processed by a grinding action. The crushing (phase I) and grinding (phase II) periods are temporally separated, however phase II facets are used during both actions (Wall et al., 2006).

However, the functional significance of phase II facets is still debated. Janis (1990) described the phase II wear facets as amorphous in nature, without sharply defined edges or directional striations.

The analysis of the occlusal load produced during phase II of the macaque chewing cycle has shown negligible forces (Hylander & Crompton, 1980; Wall et al., 2006) and small mandibular movements, suggesting that grinding during phase II movement is of minimal importance for food breakdown, with most food breakdown on phase II facets occurring during the end of phase I with a crushing action (Wall et al., 2006). Moreover, Wall et al., (2006) noted that a significant part of grinding occurs along the phase I facets during phase I. Recently, Krueger et al. (2008) proposed two alternative hypotheses to explain why the wear pattern of phase I and phase II surfaces differs: a) These differences may be related to the volume of food and associated abrasives interposed between surfaces as they contact one another, or b) could be related to the angle of masticatory forces relative to the planes of the wear facets themselves. Gordon (1984) added that wear facets present on the cusp tips of the lower molars of chimpanzees formed during puncture-crushing (Fig. 2.6e). Furthermore, Janis (1990) considered the crushing wear of upper and lower molars, dividing this into tip crushing wear and shearing crush wear. Tip crushing wear is characterized by a circular shape without directional striations, while shearing crush wear displays directional striations and the facets are more oval in shape. In contrast with tip crushing wear, shearing crush wear is most likely formed during the chewing phases, when the cusp tip interlocks with the opposing valley, functioning with a "tongue and groove" action (Janis, 1990).

Moreover, Janis (1990) also divided the phase I facets into buccal and lingual, describing the lingual facets as having an amorphous shape which is not clearly defined, and possibly related to a greater transverse component of the jaw movements.

2.6 Dental Occlusal Compass

The occlusal compass describes the interactions of antagonist cusps and basins of teeth through a three-dimensional pattern which includes the cusp's movement in all three planes of motion (Douglass & DeVreugd, 1997) (Fig. 2.7). Thus, using the occlusal compass it is possible to reconstruct the jaw movements, analysing the dental wear pattern (Douglass & DeVreugd, 1997; Schulz 2003; Schulz & Winzen, 2004; Kullmer et al., 2004, 2009; Ulhaas et al., 2007).

The occlusal interlock related to the morphology of dental relief, the type of occlusal relationship and a dependence on the degree of wear, are all factors in limiting the possible jaw movements, predetermining the pathways on which teeth can be guided against each other (Ulhaas et al., 2007). In cheek teeth with advanced wear, the elimination of interlocking cusp relations, reduces the occlusal guidance and therefore increases the degree of mandibular mobility allowing a wider range of masticatory movements (Begg & Keisling, 1877; Gordon, 1984). Moreover, the lower jaw movements are also restricted by the anatomy of the bilateral temporomandibular joint (Douglass & DeVreugd, 1997). The compass represents the possible occlusal directions depending on condylar movements (Ulhaas et al., 2007).

Starting from a position of centric occlusion, and considering only one side (a different and opposing situation will occur on the other side) the general mandibular movements are (Douglass & DeVreugd, 1997):

Laterotrusion: a laterally or outward side thrust (working path);
Mediotrusion: a medially or inward side thrust (non-working or balancing path);
Protrusion: a forward thrust;
Lateroprotrusion: an outward and forward thrust;
Medioprotrusion: an inward and forward thrust;

In addition to these general directions, the shift of the rotating condyle can generate another two horizontal movements: retrusion and immediate side shift (Schulz, 2003) (Fig. 2.7). Retrusion movement is the posterior thrust, while the immediate side shift indicates a transversal functional field on the balancing side where the condyle is medially shifted (Ulhaas et al., 2007). In addition to the horizontal movements, the condylar shift determines the possibility to produce vertical movements, such as surtrusion (upwards) and detrusion (downward), which are also important for food breakdown (Ulhaas et al., 2007). Obviously the orientation of the movement is different on the maxilla and mandible due to the perspective of each cusp in relation to the opposing arch (Douglass & DeVreugd, 1997). For example, the mandibular protrusion thrusts all cusps anteriorly over the opposing maxillary dentition, while at the same time, this jaw movement, produces a posterior thrust of maxillary cusps with respect to the opposing mandibular teeth.

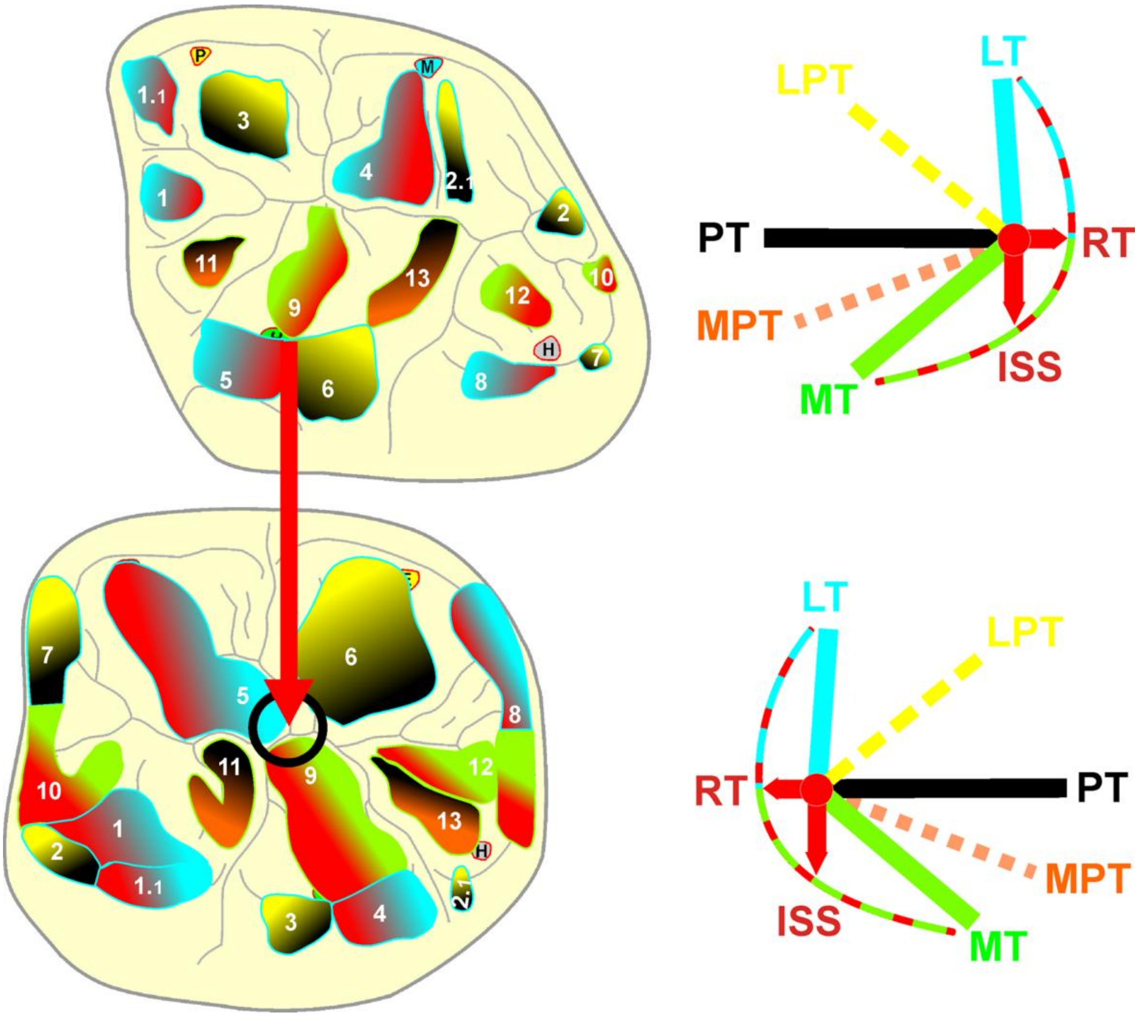


Figure 2.7 - Schematic illustration of complementary wear facets on upper and lower left first molars in an Angle class I occlusion; numerical system (1–13) after Maier and Schneck (1981). Arrow indicates occlusal relation in maximum intercuspation of protocone apex of the upper molars and central fovea of the lowers. The circle on the lower molar marks the position of the tip of the protocone during maximum intercuspation. Facet pairs 1, 4, 5, and 8 are in contact during lateroretrusion movements (blue/red). Facet pairs 2, 3, 6, and 7 correspond to lateroprotrusion (yellow/black), and facet pairs 9, 10, and 12 are in contact during mediotrusion and immediate side shift (green/red). Facet pairs 11 and 13 correspond to medioprotrusion (orange/black). Facets 7 and 10 in the lower first molar correspond with the second upper premolar, and facets 2, 7, and 10 in the upper first molar are in contact with the second lower molar. To the right, dental occlusal compass (after Schulz, 2003) shows major directions of horizontal occlusal movements for upper molars (above) and lower molars (below), laterotrusion (LT), retrusion (RT), lateroprotrusion (LPT), protrusion (PT), medioprotrusion (MPT), mediotrusion (MT), and immediate side shift (ISS); e.g., the occlusal compass illustrates the directed distally protrusive pathway of protocone cusp in the lower molar and mesially in the upper molar (from Kullmer et al., 2009).

During the chewing cycle the jaw movements and the resulting occlusal contacts are tightly related, meaning the information obtained from the analysis of the occlusal compass can be utilised to understand how wear facets are formed and what movements are responsible for the contacts on the occlusal surface (Ulhaas et al., 2007) (Fig. 2.7).

2.7 Relation between Diet and Tooth Wear

Size and shape of teeth reflect the functional demands produced by the selective pressure of the physical properties of the food ingested (Lucas, 2004). Different types of food with different physical properties require different tooth morphology to break them down (Ungar & Williamson, 2000). For instance, frugivore primates tend to have large frontal teeth for ingesting fruits and simple cheek teeth characterized by low and smooth cusps for crushing and pulping soft fruits, while folivore primates possess small frontal teeth and molar with well-developed shearing crests for cutting leaves (Fleagle, 1988) (Fig. 2.8).

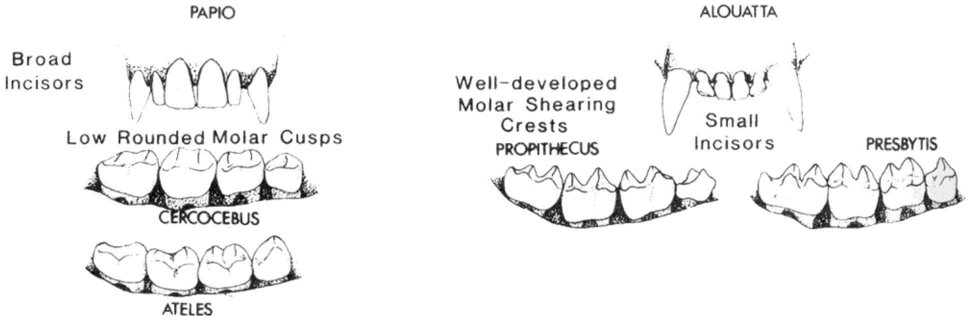


Figure 2.8 - Tooth-shape morphology in frugivorous (*Papio*, *Cercocebus* and *Ateles*) and folivorous (*Alouatta*, *Propithecus* and *Presbytis*) non-human primates (from *Fleagle*, 1988).

Thus, it is possible to compare the dental morphology of living mammals with those of extinct species in order to reconstruct their diet. However most of these studies focused on unworn teeth because they are easier to characterize and compare among different species (Ungar & Williamson, 2000). While the shape of unworn teeth can suggest what a tooth is capable of processing, tooth wear can tell us how a tooth was actually used (Teaford, 2007). Tooth wear is an inevitable process. When the masticatory cycle starts, the contact with abrasive food particles and the occlusal contact between upper and lower dentition during the chewing phase, determine a loss of a superficial enamel substance and the teeth begins to wear down. Teaford & Walker (1983) have shown that the molars of the guinea pigs were already worn before birth. Wear changes and re-shapes the primary dental morphology, producing a secondary relief. For example, in most herbivores in order to achieve a functional tooth shape, the cheek teeth must wear. In fact the dentition is designed to expose dentin (or in some case even cement) as soon as possible, allowing the enamel ridges, which wear at slower rate, to protrude above the rest of the crown and act as short blades on the thin vegetation (Lucas, 2004). Moreover, in the fossil record, most of the teeth are worn. Tooth wear is strictly connected to diet. While abrasion produces wear by the direct contact between food and tooth surface, attrition is created during the chewing phase which varies in frequency, duration and jaw movements depending on the physical property of food ingested. It is therefore essential to consider tooth wear in order to obtain information about diet.

Tooth wear can be considered at three different scales: microwear, wear facet developmentand mesowear (Janis, 1990; Fortelius & Solounias, 2000; Joomun et al., 2008) (Fig. 2.9).

Wear facets and mesowear are visible to the naked eye or at low magnification, while microwear is visible only under microscope. Density, pattern and orientation of microscopic scratches and pits that cover the tooth surface yield information about diet. The orientation of the striations on the incisors reflects the direction of preferred movement of food across the incisors (Walker, 1976; Rose et al., 1981; Ryan, 1981; Ungar, 1994), while the orientation of the scratches on the occlusal surface reflect the orientation of jaw movements (Butler, 1952; Mills, 1955, 1963; Gordon, 1984; Rensberger, 1986; Young & Robson, 1987; Young et al., 1990; Morel et al., 1991) and the orientation of tooth-food-tooth movements (e.g. Ryan, 1979; Teaford & Walker, 1983; Walker, 1984; Teaford & Byrd, 1989). The density and size of the microwear features reflect the toughness of food. For example, primates that eat hard objects usually show large pits on their molars, while folivores tend to have relatively more scratches than pits on their molar (Teaford & Walker, 1984; Teaford, 1988, 2007). The use of microwear analysis was extended also to reconstruct the diet of the extinct hominid species, from the Pliocene australopithecines to the more recent Neanderthal, and to compare archaeological *Homo sapiens* populations that relied on different food sources, or to compare populations during the transition from a hunter-gatherer to agriculture subsistence.

The studies on a variety of mammals have shown that the type of wear and the relative sizes of the different facets can be related to the diet of the mammal in question (e.g. Butler ,1952, 1973; Kay, 1977; Janis, 1990). In comparing mammals with similar dental morphology, differences in diet will produce different wear patterns, while mammals with a similar diet but with a different dental morphology, will show similar wear patterns (Janis, 1990).

The proportion of crushing and shearing wear in mammals teeth have been extensively used for dietary interpretations (e.g. Kay & Hiiemae, 1974; Kay & Hylander, 1978; Maier, 1980; Janis 1979, 1990; Van Valkenburgh, 1989).

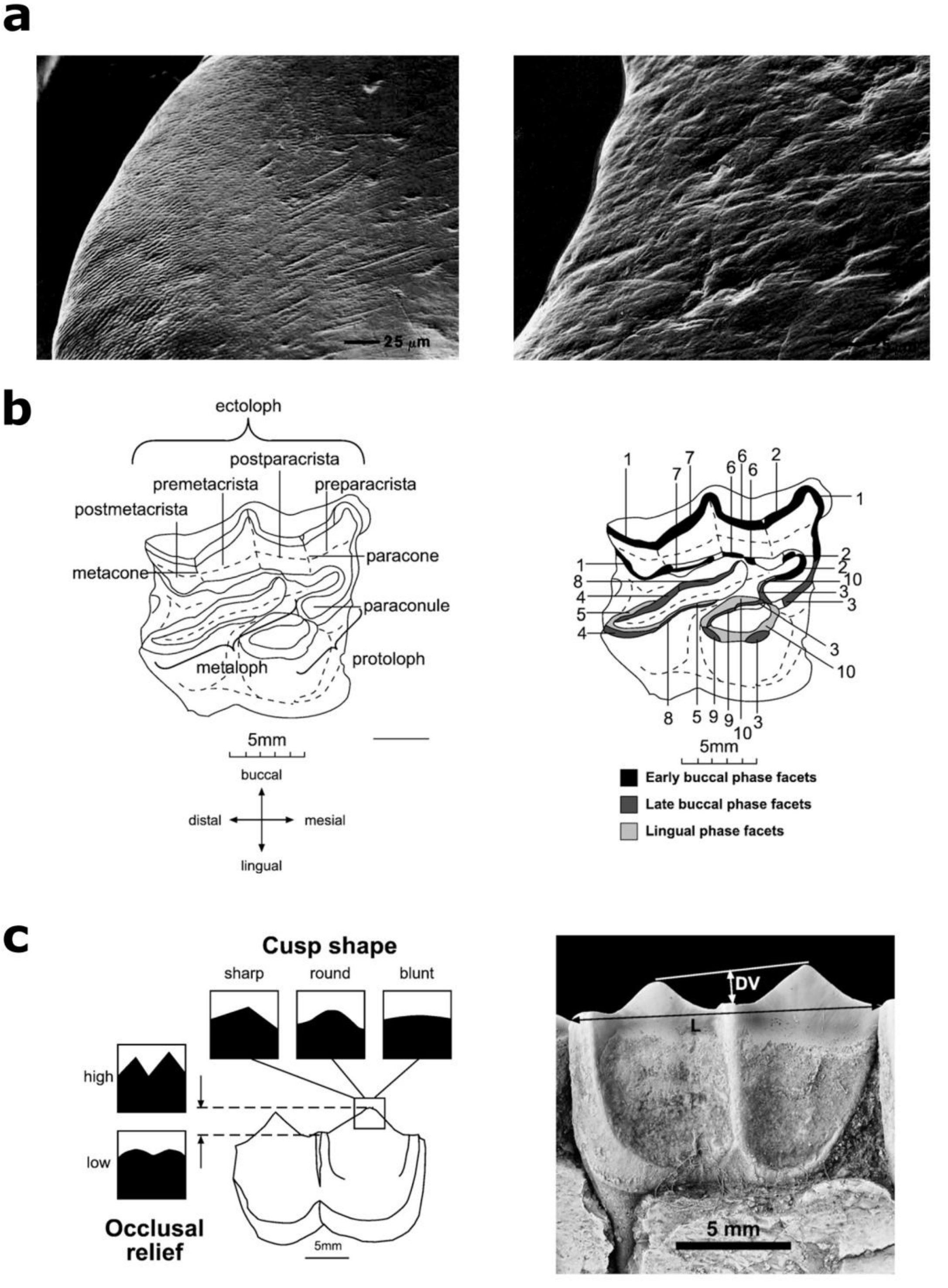


Figure 2.9 - Study of tooth wear at three different scales: a) microwear, b) wear facets (or macrowear) and c) mesowear. Figure modified from Teaford & Walker (1984) and from Joomun et al. (2008).

Carnivores that rely on a high carnivorous diet, such as felids, show almost solely shearing wear, while carnivores which include a certain proportion of vegetables in their diet, such as canids, display a higher proportion of crushing wear (Van Valkenburgh, 1989). Herbivores with a more fibrous diet show an increase in buccal phase I facets and a decrease in lingual phase I facets (Janis, 1990). Morevoer the development of phase II wear in herbivores appears to be correlated with the inclusion of fruit in the diet, and is reduced or absent in more strictly folivorous species (Janis, 1990). In primates, such as the genus Colobus, with a diet constitutes mostly by seeds, the crushing facets will be especially prominent, while a more folivorous diet it will reflect a decrease in crushing wear and an increase of shearing wear (Janis, 1990). The analysis of form and pattern of tooth wear was used by Molnar (1972) to interpret the diet and the cultural habits of prehistoric human populations. Smith (1984) considered the flatness of molar wear in order to evaluate the differences between hunter-gatherers and agriculturalist. The molar wear pattern of hunter-gatherers is characterized by a flatter tooth surface due to the mastication of tough and fibrous stuff, while agriculturalists show a more restricted wear pattern with a more oblique wear planes caused by the reduction of toughness and fibrousness in the diet (Smith, 1984). Ulhaas et al. (2007) analyzed the occlusal wear pattern employing a 3D virtual approach, comparing the molars of *Australopithecus africanus*, *Australopithecus afarensis* and *Paranthropus robustus*. Although all the three species showed a similar overall wear pattern, in details the wear pattern results to be different. The molars of *A. afarensis* present well-developed shearing crest, which probably reflects a fibrous and tough diet, including some quantity of meat. *P. robustus* instead shows a pronounced flattening of the tooth crown with a greater intraspecific variation, probably due to an omnivorous diet including hard objects as fall-back food. The wear pattern in *A. africanus* shows a high variability, indicating the possibility of the exploitation of both hard and brittle food.

Mesowear represents an intermediate level between microwear and wear facets, based on facet development on the occlusal surface of the teeth considering the cusp relief and cusp shape (Fortelius & Solounias, 2000). Mesowear analysis allows evaluating the relative roles of attrition and abrasion in shaping tooth cusp morphology over an animal's lifetime (Fortelius & Solounias, 2000; Croft & Weinstein, 2008). It was primarily used to reconstruct the paleodiet of extinct species based on the mesowear features of extant mammals. For instance, the mesowear analysis of extant ungulates permitted to separate successfully these species into the conventional dietary categories of browser, grazer and mixed feeder (Fortelius & Solounias, 2000).

2.8 A New Approach to Reconstruct the Diet of Neanderthals

The reconstruction of the Neanderthal diet and his ecology has been mostly based on the analysis of faunal assemblage, stone tool technology, dental microwear and isotopic signatures. However, these methods are affected by some limitations. Although the study of the animal remains can indicate hunting or scavenging episodes, it cannot give information about the diet composition over the long term (Richards et al., 2000). Isotopic methods are destructive, requiring the removal of tissues from bones and teeth of precious and rare fossils as those of Neanderthals. In addition, stable isotopes analysis requires good collagen preservation, limiting the number of Neanderthal specimens that can be analyzed. The reconstruction of the diet using dental microwear is based on the analysis of microscopic scratches and pits. These microwear features in fossil teeth could be due to postmortem processes or produced during chewing. However, postmortem wear results to be difficult to identify at low magnification and his presence reduces the number of specimens which can be analyzed using scanning electron microscope (Teaford, 2007). Moreover microwear analysis of the tooth surface only reflects wear that has occurred relatively recently (Janis, 1990). Teaford & Oyen (1989a, 1989b), analysing the dental microwear of living vervet monkeys feeding on hard and soft diets, noted that the microwear pattern could change in relation to diet, in one or two weeks. This phenomenon has been called "The Last Supper" by Grine (1986), and it could be particularly evident for species whose diets undergo seasonal alteration. Thus, the study of dental microwear in fossils, could reflect the diet of the last period of their lives, which could coincide with a "bad" season, and therefore it could not indicate their typical diet (Janis, 1990). Differently from the microwear, the gross dental wear is a cumulative process which occurs during the lifespan of the animal, and thus reflects the diet over a long term (Janis, 1990).

In this study, we evaluate the functional aspect of the occlusal surface of Neanderthal and early *Homo sapiens* (EHS) dentition by means of a new method based on the analysis of high resolution three-dimensional virtual models of teeth (Kullmer et al., 2002, 2004, 2009; Ulhaas et al., 2004, 2007). The analysis and quantification of the wear facets, such as the mapping distributions (or topography) of the occlusal contacts, the relative areas, the relief index and the inclination of the plane of the facet all provide information about the dynamics of the occlusal relationships and their function. Moreover, the addition of the occlusal compass analysis, allows reconstruction of the mandibular movements responsible for the contacts created during the chewing cycle. Since jaw movements and diet are strictly related, the results obtained can be used to interpret the diet of the two Pleistocene hominids.

The fossil sample consists of worn teeth of specimens from different geographical areas that lived in different climatic conditions at different times, overcoming the limits of the stable isotopes analysis which were based only on Neanderthal specimens from cold environments. Furthermore, this new approach goes beyond the dental functional morphology analysis based on unworn teeth only, and is not limited by the presence of postmortem microscopic features that reduce the number of specimens which can be used for microwear analysis.

In order to evaluate the importance of meat in the diet of Neanderthals, we use a comparative sample constituted by the dentition of modern hunter-gatherers collected from different museums, which relied heavily on animal proteins such as Inuit, Vancouver Islanders and Fuegians. Additionally, the dentition of modern hunter-gatherers with a mixed diet such as Australian aborigines and Bushmen, have also been included in the analysis. If Neanderthals had a diet consisting almost solely of animal proteins, they should show a similar wear pattern to those of the carnivorous hunter-gatherers.

If the occlusal wear pattern of Neanderthal and EHS will differ, the next step will be to understand the possible causes. Are these differences caused by the different tooth morphology between the two hominid species or are they due to a different diet? Does the wear pattern change in relation to the use of different stone tool technology (e.g. Mousterian versus Auchelian)? Are Neanderthals characterized by a homogenous wear pattern, or are there any differences between Neanderthals from cold and warm environments?

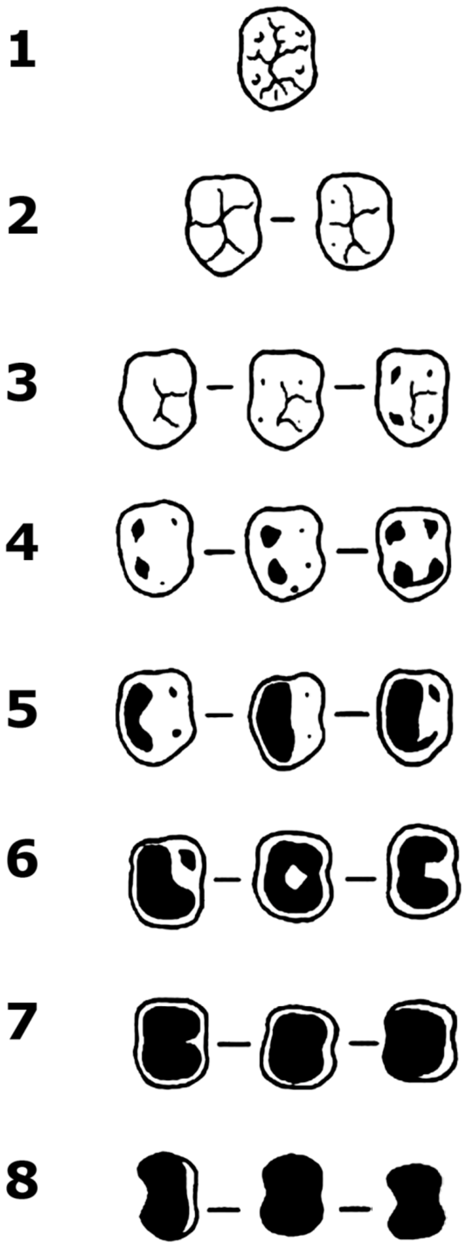
Chapter 3

Materials

3.1 Introduction

Occlusal wear pattern analysis was carried out on digital 3D models which were generated thru the surface scanning of Neanderthal and early *Homo sapiens* maxillary molar casts. Virtual 3D models were also generated from casts of modern hunter-gatherer molars whose diet is known and therefore have been included in the analysis as a comparative sample. Mandibular molars were not considered as mandibles were often absent from the sample specimens and thus enough molars were not available to create a robust lower molar sample set. The third upper molars were characterized by an extreme variability and consequently have been discarded. We have included only slightly worn molars where facets were identifiable and did not coalesce. The degree of wear was determined by evaluating the amount of dentin exposure and cusp removal according to the wear score system created by Smith (1984) (Fig. 3.1). In order to have a more homogenous sample, from each specimen we selected only one maxillary molar based on its degree of wear (between stage 2 and 3). If the left M^1 was absent, we used the right M^1 and if both left and right M^1's were absent or presented too high a degree of wear, we selected the M^2 giving priority to the left side.

The sample is comprised of 73 specimens, whereof 19 are Neanderthals, 12 are early *Homo sapiens*, and 42 are of modern hunter-gatherers. The sample contains 40 first upper molars (41.1% left and 13.7% right) and 33 second upper molars (35.6% left and 9.6% right), and is characterized by a stage of wear 2 (36%) and a stage of wear 3 (64%) (Fig. 3.2). Since left molars were more numerous, for the orientation the left side was preferred, and the right molars were mirrored.



1. Unworn to polished or small facets (no dentin exposure)
2. Moderate cusp removal (blunting).Thinly enamelled teeth show no more than one or two pinpoint exposures
3. Full cusp removal and/or some dentin exposure, pinpoint to moderate
4. Several large dentin exposures, still discrete
5. Two dentinal areas coalesced
6. Three dentinal areas coalesced, or four coalesced with enamel island
7. Dentin exposure on entire surface, enamel rim largely intact
8. Severe loss of crown height, breakdown of enamel rim; crown surface takes on shape of roots

Figure 3.1 - Schematic illustration in occlusal view of lower molars representing the different wear stages (1-8). Dentin exposures are depicted in black (modified from Smith, 1984).

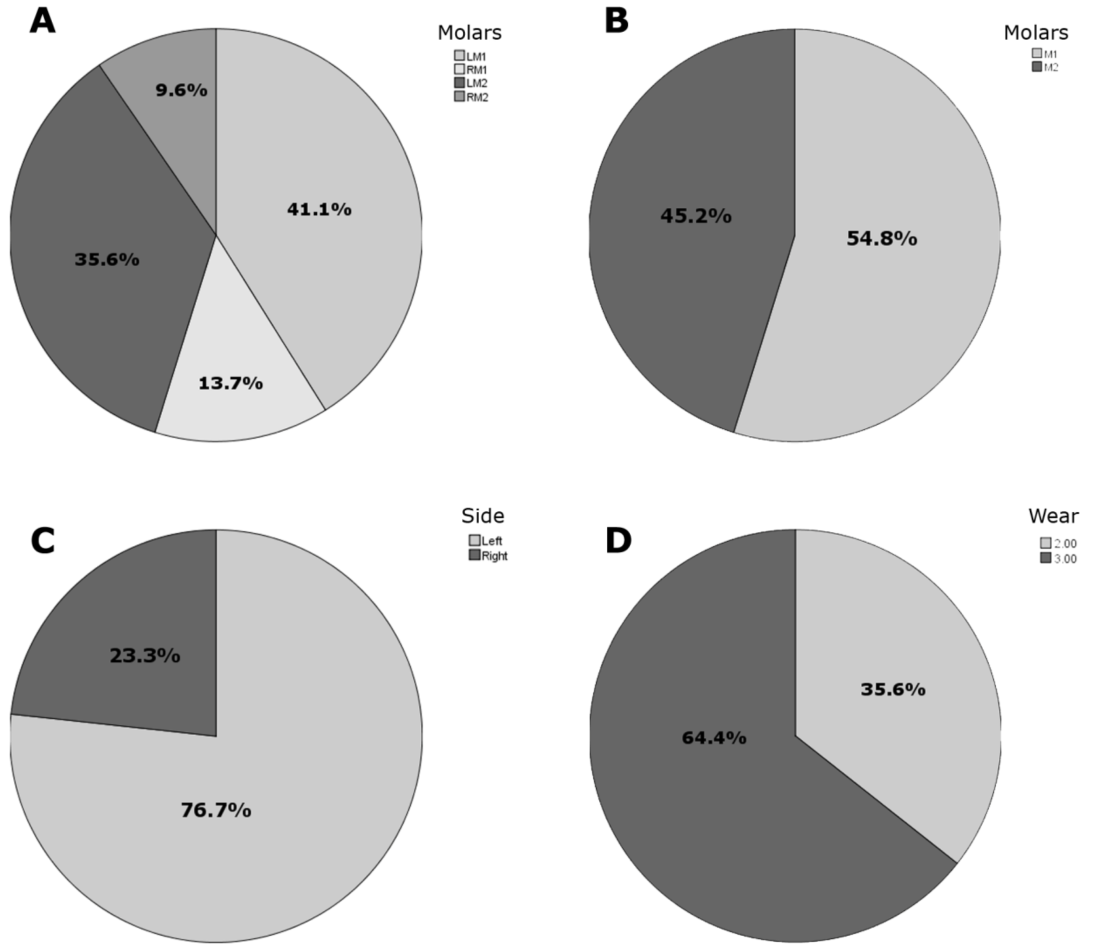


Figure 3.2 - Pie charts representing the entire sample used, illustrating the percentages of molar types (A and B), side (C) and degree of wear (D).

3.2 Neanderthals and early *Homo sapiens* sample

The fossil sample consists of 31 first and second upper molars, whereof 19 are Neanderthals (Tab. 3.1) and 12 are early *Homo sapiens* (Tab. 3.2). For each specimen information is provided on the tooth type, wear stage, geographical area, approximate dating, including brief description of the site and the landscape morphology per cited literature, and the corresponding Oxygen Isotope Stage (OIS) based on the SPECMAC of Van Andel & Tzedakis (1996) (Fig. 3.3). Paleoenvironmental information derived thru faunal analysis, palynological data and pedology, have also been included. The reconstruction of the vegetation was mostly based on the work of Van Andel & Tzedakis (1996), which described the European vegetation at different Oxygent Isotope Stages (Fig. 3.4, 3.5 and 3.6). Moreover, where the data was available, explicit dietary information is provided. In addition, they are also included information about the repository, and if the casts used have been generated from moulds of the original dentition or from casts.

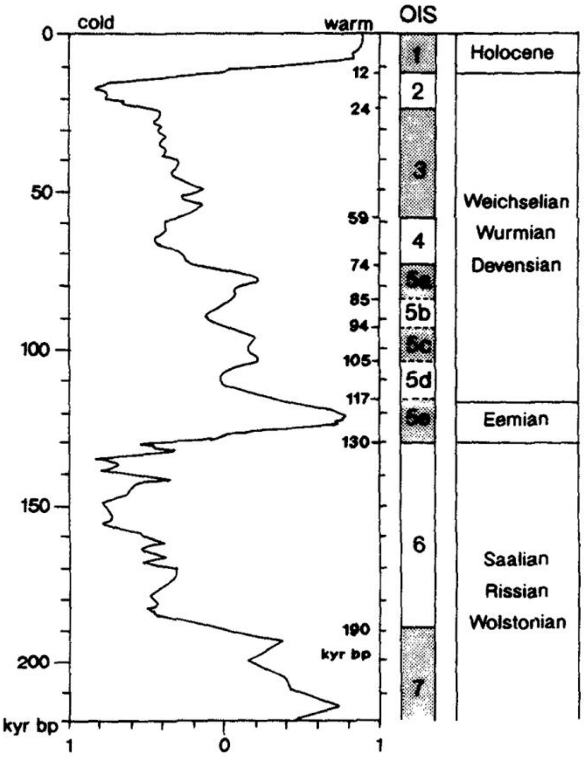


Figure 3.3 - SPECMAC (Orbital-based global chrono-stratigraphy) of the last 200,000 years, illustrating the climatic oscillations (warm intervals are shaded) during the different Oxygen Isotopic Stages (OIS). Age in millennia (kyr) (from Van Andel & Tzedakis, 1996).

3.2.1 Neanderthals

Krapina

This Neanderthal assemblage is the most numerous individual sample included in our analysis and consists of 12 specimens (Krapina 47, 48, 134, 136, 165, 166, 167, 169, 171, 172, 175, and 177). The site is a rock shelter facing the River Krapinica at an altitude of 120 m above sea level and located near the village of Krapina in Northern Croatia. The fossils have been dated to 130,000 ± 10,000 BP (Rink et al., 1995) which corresponds to OIS 5e and indicates an interglacial period characterized by a warm climate (Fig. 3.4). The Croatian environment was dominated by deciduous forests and Mediterranean evergreen woodland (Van Andel &

Tzedakis, 1996). The faunal remains consisted of: *Dicerorhinus kirchbergensis*, *Ursus spelaeus*, *Arctomys marmot*, *Canis lupus*, *Felis catus*, *Ursus arctos*, *Equus caballus*, *Sus scrofa*, *Cervus elaphus* and *Bos* or *Bison*. *C. elephas* was rare, and skeletal remains of *Testudo* have been also found (Oakley et al., 1971). Based on the study of the faunal assemblage, the Krapina Neanderthals have been hypothesized as active hunters of large herbivores including the Merck's rhinoceros (Miracle, 1999; Karavanić, 2004).

Repository (casts): Department of Physical Anthropology at Washington University in St. Louis, USA.

Table 3.1 - List of Neanderthal specimens used, including information about tooth type, degree of wear, locality, dating, Oxygen Isotopic Stage (OIS), repository and if the moulding was made using the original dentition or a dental cast. Repository: 1) Natural History Museum of London, England; 2) Department of Physical Anthropology at Washington University in St. Louis, USA; 3) Department of Anatomy and Anthropology at the University of Tel Aviv, Israel; 4) Museum for Prehistory and Early History of Berlin, Germany.

Specimen	Tooth	Wear	Locality	Dating	OIS	Repository	Moulding
Krapina 47	ULM1	2	Croatia	130 ± 10	5e	2	cast
Krapina 48	ULM1	2	Croatia	130 ± 10	5e	2	cast
Krapina 134	URM1	2	Croatia	130 ± 10	5e	2	cast
Krapina 136	ULM1	2	Croatia	130 ± 10	5e	2	cast
Krapina 165	URM2	2	Croatia	130 ± 10	5e	2	cast
Krapina 166	URM1	2	Croatia	130 ± 10	5e	2	cast
Krapina 167	URM1	2	Croatia	130 ± 10	5e	2	cast
Krapina 169	URM2	2	Croatia	130 ± 10	5e	2	cast
Krapina 171	URM1	2	Croatia	130 ± 10	5e	2	cast
Krapina 172	URM2	3	Croatia	130 ± 10	5e	2	cast
Krapina 175	ULM2	2	Croatia	130 ± 10	5e	2	cast
Krapina 177	URM2	2	Croatia	130 ± 10	5e	2	cast
Tabun 1	ULM2	3	Israel	122 ± 16	5e	1	cast
Monsempron 2	ULM1	3	Southern France	100-120	5e	2	cast
Monsempron 3	URM1	3	Southern France	100-120	5e	2	cast
Shanidar 2	ULM2	3	Iraq	?	?	2	cast
Amud 1	ULM2	3	Israel	55	3	3	original
Vindija V259	ULM2	2	Croatia	42	3	2	cast
Le Moustier 1	ULM1	2	Central France	41	3	4	original

Tabun

Tabun 1 was discovered inside the Tabun Cave 20 km south of Haifa, Israel and situated on the western cliff of Mount Carmel at 60 m above sea level facing the Mediterranean coast, (Tsatskin, 1998). The skeletal remains were dated to 122,000 ± 16,000 (Grün & Stringer, 2000), corresponding to OIS 5e, where the Levantine territory was characterized by a warmer climate, covered by a Mediterranean vegetation (Van Andel & Tzedakis, 1996) (Fig. 3.4).

Repository (casts): Natural History Museum of London, England.

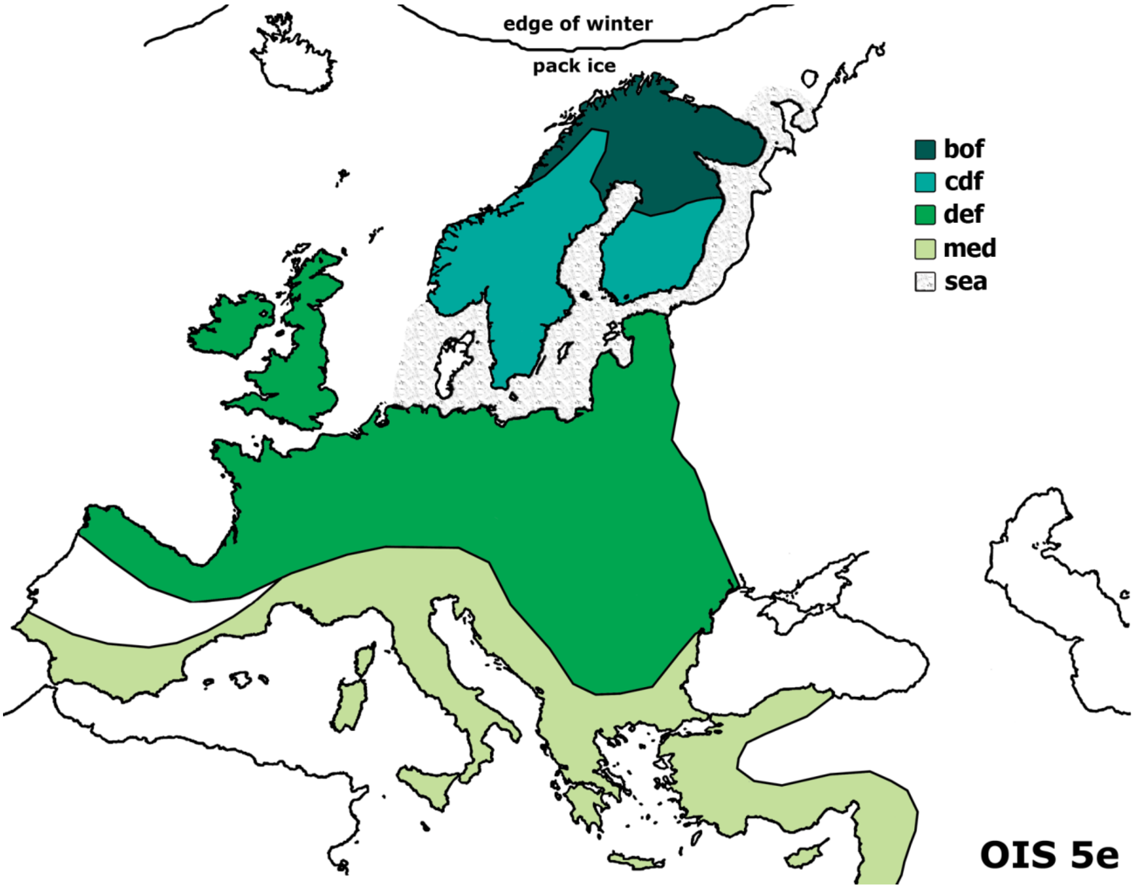


Figure 3.4 - Map of Europe during the optimum of the last interglacial (OIS5e) at 120,000-125,000 BP (modified from Van Andel & Tzedakis, 1996). Palaeoenvironments: boreal forest (bof); mixed conifer and deciduous forest (cdf); deciduous forest (def); Mediterranean evergreen woodland (med); Eemian/Baltic Sea (sea).

Monsempron

The skeletal remains (Monsempron 2 and 3) were found in a karstic cave in the area of Monsempron 25 km north-east of Villeneuve-Sur-Lot in Southern France. The presence of Quina Mousterian tools found beneath upper, Paleolithic layers would suggest an occupation during OIS 4 (Fig. 3.5) or beginning of OIS 3 (Quintard et al., 2007). The faunal assemblage consisted of: *Canis lupus*, *Vulpes vulpes*, *Hyaena crocuta spelaea*, *Rangifer tarandus*, *Equus caballus*, *Bos primigenius* and *Bison* (Oakley et al., 1971), indicating the presence of a cold and open environment.

Repository (casts): Department of Physical Anthropology at Washington University in St. Louis, USA.

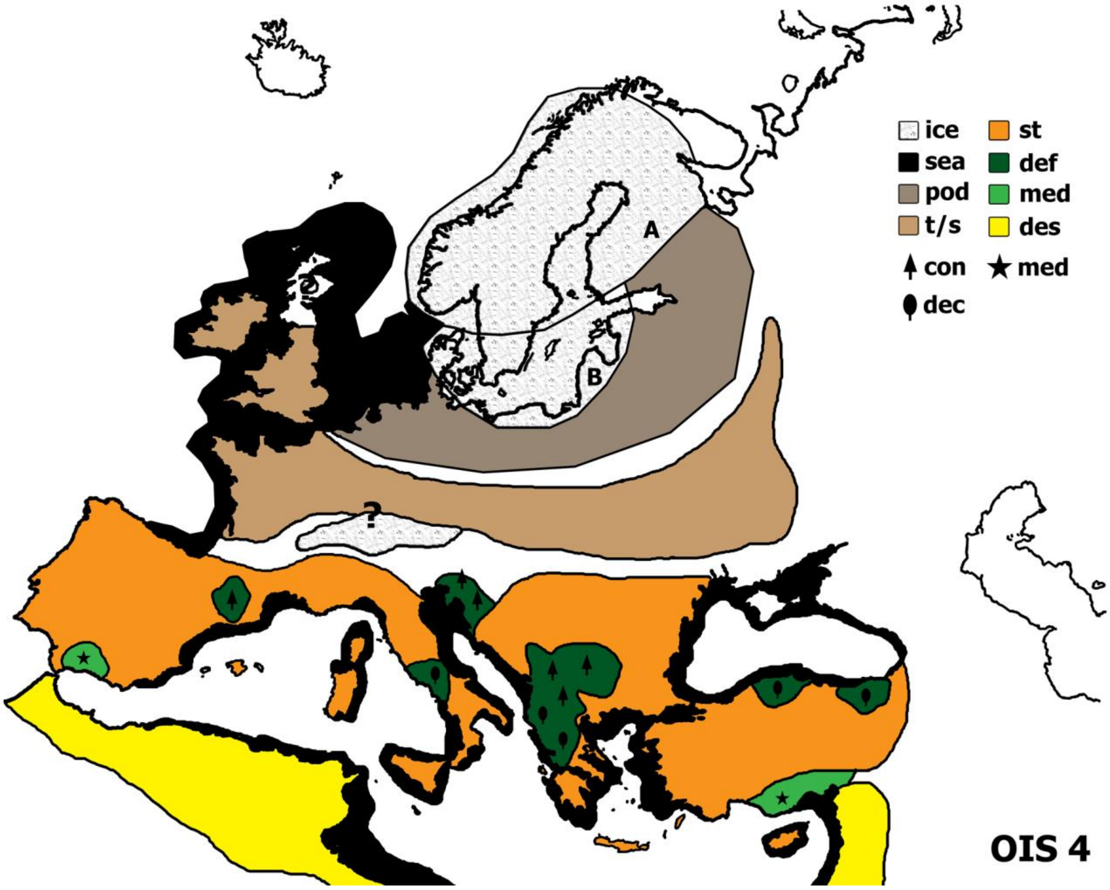


Figure 3.5 - Map of Europe at 65,000 BP (late OIS 4). Palaeoenvironments: ice-sheet (ice); emerged coastal plains (sea); polar desert (pod); tundra cold steppe mosaic (t/s); arid cold steppe (st); deciduous forest (def); Mediterranean evergreen (med); desert (des); coniferous forest (con) (modified from Van Andel & Tzedakis, 1996).

Shanidar

The sample consists of one specimen (Shanidar 2) discovered in a cave along the Shanidar Valley at an altitude of 765 m above sea level and located in northeastern Iraq (Trinkaus, 1983). The Shanidar 1 and 5 have been dated around 45,000 BP (Vogel & Waterlbolk, 1963), while the other specimens are probably much older belonging to the period comprising OIS 4 (Fig. 3.4) and 6 (Cowgill et al., 2007). The associated faunal remains were dominated by wild goat, red deer, roe deer, wild boar, and tortoise (Trinkaus, 1983). The Shanidar Neanderthals also exploited plant materials as highlighted by the presence of plant microfossils trapped in the dental calculum of Shanidar 3 (Henry & Piperno, 2008).

Repository (casts): Department of Physical Anthropology at Washington University in St. Louis, USA.

Amud

Human remains (Amud 1) were discovered in the Amud cave of Israel and is located on the margins of the Dead Sea Rift Valley 5 km to the northwest of the Sea of Galilee at depth of 110 m below sea level (Madella et al., 2002). They have been dated around 55,000 BP (Valladas et al., 1999). The climate was characterized by colder and wetter conditions than those present during OIS5, with marked summer rainfalls, and dense forest cover (Hallin, 2002, 2008). The associated faunal remains are dominated by gazelle, fallow deer and wild goat, while large species rarely occur (Rabinovich & Hovers, 2004). Moreover, analysis of phytoliths found in the Amud deposit cave indicate that these individuals exploited various types of vegetable matter including palm, figs and grass seeds (Madella et al., 2002).

Repository (original): Department of Anatomy and Anthropology at the University of Tel Aviv, Israel.

Vindija

The open air site of Vindija, northern Croatia is situated near a cave located in semi-mountainous terrain at 275 m above sea level (Wolpoff et al., 1981). The human occupation has been dated between 28,000 and 42,000 BP (Krings et al., 2000; Higham et al., 2006). The specimen included in our sample (Vindija V259) belongs to the G_3 layer, dated at 42,000 BP. The vegetation was dominated by temperate taxa (Genty et al., 2005) (Fig. 3.6). Stable isotope analysis of bone collagen indicates a diet based almost exclusively on animal food sources (Richards et al., 2000).

Repository (casts): Department of Physical Anthropology at Washington University in St. Louis, USA.

Le Moustier

These remains (Le Moustier 1) belong to an adolescent found in the Lower cave of Le Moustier in the Dordogne region of France (Thompson & Illerhaus, 1998). They are dated to ~41,000 BP (Mellars & Grün, 1991) and correspond to the cold interval of OIS 3 (Valladas et al., 1986) (Fig. 3.6). The faunal assemblage was composed of *Equus sp.*, cervids (including *Rangifer tarandus*) and bovids (Oakley et al., 1971).

Repository (original): Museum for Prehistory and early History of Berlin, Germany.

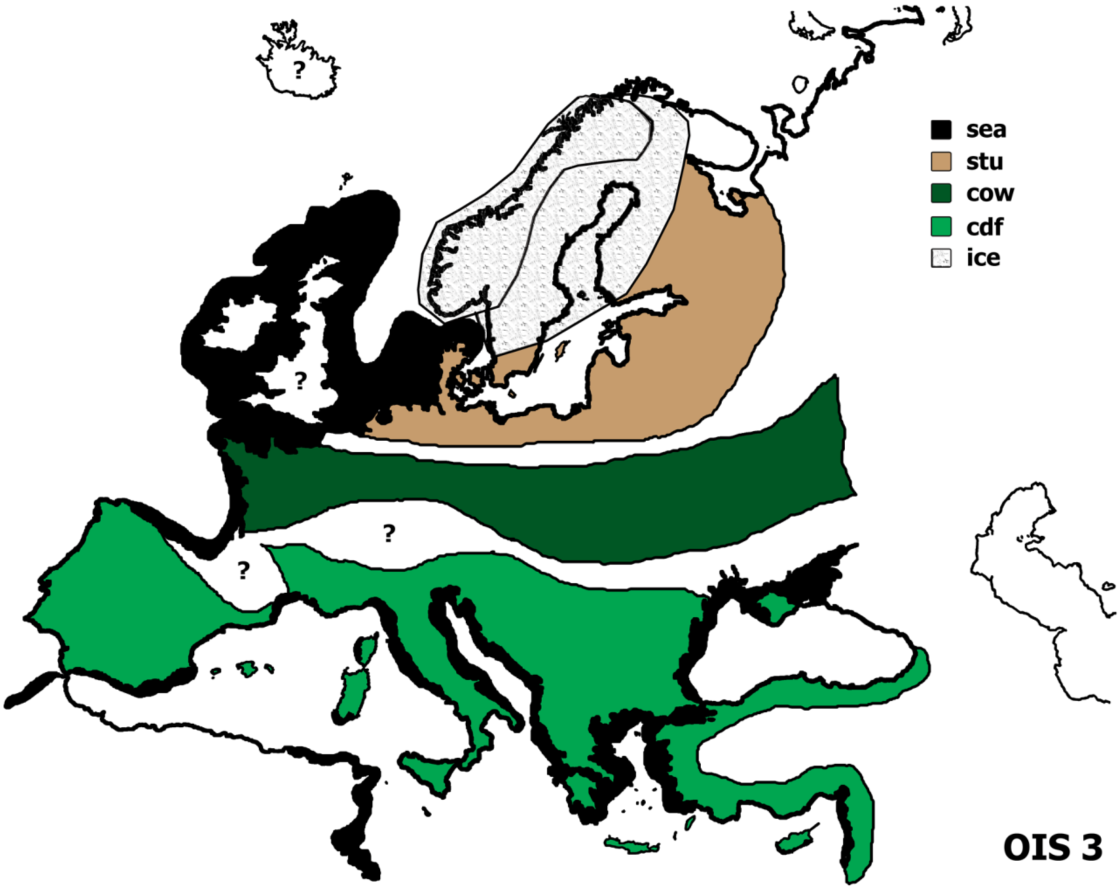


Figure 3.6 - Map of Europe during a warm phase of OIS 3 at 36,000-39,000 BP (modified from Van Andel & Tzedakis, 1996). Palaeoenvironments: emerged coastal plains (sea); shrub tundra (stu); conifer woodland (cow); mixed conifer and deciduous forest (cdf); ice-sheets (ice).

3.2.2 Early Homo sapiens

Qafzeh

The sample consists of seven specimens (Qafzeh 5, 6, 7, 9, 11, 15 and 27) discovered in a cave in the Qafzeh Mountains located near Nazarteth in the Lower Gallilee, Israel (Bar-Yosef Mayer et al., 2009). The human fossils have been dated to 115,000 ± 15,000 BP (Schwarz et al., 1988). The sea level was about 40 to 80 m below the current msl (Waelbroeck et al., 2002; Siddall et al., 2003). The climate was hot and dry (similar to present-day conditions), with limited or no rains in summer (Hallin et al., 2008). The faunal assemblage is dominated by red deer, fallow deer and aurochs (Rabinovich et al., 2004). Recently, marine shellfish have been found associated with the remains indicating the exploitation of broader food resources (Bar-Yosef Mayer et al., 2009).

Repository (original): Department of Anatomy and Anthropology at the University of Tel Aviv, Israel (Qafzeh 9 and 11).

Repository (casts): Department of Physical Anthropology at Washington University in St. Louis, USA (Qafzeh 5, 6, 7, 15 and 27).

Table 3.2 - List of early *Homo sapiens* specimens used, including information about tooth type, degree of wear, geographical origin, dating, Oxygen Isotopic Stage (OIS), repository and if the moulding was made using the original dentition or a dental cast. Repository: 2) Department of Physical Anthropology at Washington University in St. Louis, USA; 3) Department of Anatomy and Anthropology at the University of Tel Aviv, Israel; 5) Natural History Museum of Vienna, Austria; 6) Museum of Balzi Rossi in Ventimiglia, Italy; 7) Department of Anthropology, University of Vienna, Austria.

Specimen	Tooth	Wear	Locality	Dating	OIS	Repository	Moulding
Qafzeh 5	ULM1	3	Israel	115,000 ± 15,000	5d	2	cast
Qafzeh 6	ULM2	3	Israel	115,000 ± 15,000	5d	2	cast
Qafzeh 7	ULM2	3	Israel	115,000 ± 15,000	5d	2	cast
Qafzeh 9	ULM1	3	Israel	115,000 ± 15,000	5d	3	original
Qafzeh 11	ULM1	2	Israel	115,000 ± 15,000	5d	3	original
Qafzeh 15	URM1	2	Israel	115,000 ± 15,000	5d	2	cast
Qafzeh 27	ULM1	3	Israel	115,000 ± 15,000	5d	2	cast
Mladec 2	ULM1	3	Czech Republic	31,000	3	5	original
Barma Grande 3	ULM1	2	Italy	24,800	3	6	original
Barma Grande 4	ULM1	3	Italy	24,800	3	6	original
Sungir 2	URM1	2	Russia	26,200 - 27,200	3	7	cast
Pataud 224	ULM1	3	Central France	21,000 - 22,000	2	2	cast

Mladeč

These early *Homo sapiens* remains (Mladeč 2) dated ~31,000 BP (Wild et al., 2005) were found in a karstic cave inside Třesín Hill at an altitude of 343 m above sea level, and located in central Moravia, Czech Republic (Svoboda, 2001). The faunal remains were composed mainly of *Rangifer tarandus*, *Bison priscus* and *Equus sp.* (Pacher, 2006).

Repository (originals): Natural History Museum of Vienna, Austria.

Barma Grande

The sample is composed of two specimens (Barma Grande 3 and 4) discovered in the Grimaldi Caves (a complex of caves and rock shelters) situated along the cliffs of Balzi Rossi at the western end of the Liguria region, Italy. The remains have been dated around 25,000 BP (Formicola et al., 2004). The faunal assemblage was comprised primarily of *Ursus spelaeus*, *Cervus elaphus*, *Bos primigenius*, *Capra primigenia* and *Strombus bubonius* (Oakley et al., 1971; Alciati et al., 2005), with the addition of large quantities of marine shellfish (Stiner, 1999). The vegetation was mostly characterized by open environments and in less quantity by coniferous forests (Follieri et al. 1998; Watts et al. 1996).

Repository (originals): Museum of Balzi Rossi in Ventimiglia, Italy.

Sungir

Remains were found at Sungir in the plains of Central Russia near the village of Vladimir, 200 km north-east of Moscow, and dated between 19,000 and 27,000 BP (Kuzmin et al., 2004). The occupation of the site occurs between the end of OIS 3 and the beginning of OIS 2, when Northern Europe was characterized by a cold, dry, continental climate dominated by steppe vegetation and pine tree forests (Buzhilova, 2005). The Sungir faunal assemblage is typical of these cold environments and composed of mammoths, polar fox, and reindeer or *Saiga* (Oakley et al., 1971).

Repository (cast): Department of Anthropology, University of Vienna, Austria.

Pataud

The site of Abri Pataud is a rock shelter formed in a limestone cliff facing the Vézère river at an altitude of 66 m above sea level and located in the Aquitaine region in southwestern France (Théry-Parisot, 2002). The site was occupied between 21,000 to 28,000 BP (Mellars et al., 1987) with Pataud 224 dated around 22,000 BP. The landscape was characterized by open woodland and a cold-dry climate dominated by *Pinus sylvestris*, shrubs and *Salix sp.* along the riverbanks (Théry-Parisot, 2002).

Repository (casts): Department of Physical Anthropology at Washington University in St. Louis, USA

3.3 Modern hunter-gatherers sample

The modern hunter-gatherer sample consists of 42 specimens; 10 Inuit, 15 Vancouver Islanders, 7 Fuegians, 3 Australian aborigines and 7 Bushmen (Tab. 3.3). Inuit, Vancouver Islanders and Fuegians subsisted on a diet based mostly on the exploitation of animal proteins while Australian aborigines and Bushmen have a mixed diet of plant and animal materials. All of these dental casts were produced from moulds of the original specimens.

Bushmen

The sample consists of seven specimens attributed to the Khoisan group coming from the Kalahari and Cape Region, and were collected by Rudolph Pöch during his trips to South Africa between 1907 and 1909 (Pacher, 1961) (Fig. 3.7).

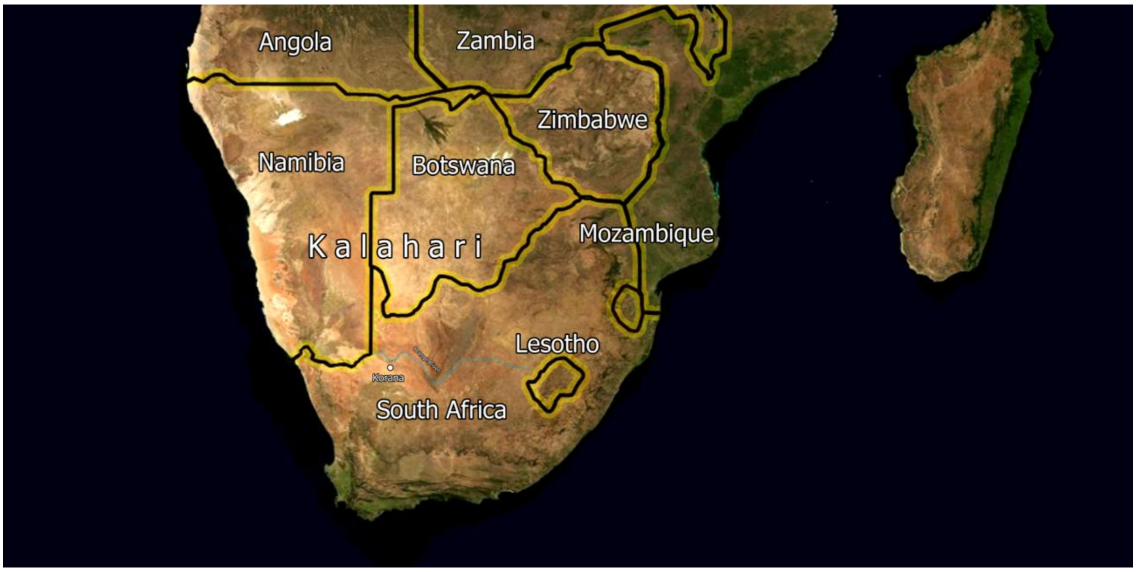


Figure 3.7 - Bushmen geographical map (modified from © 2009 Microsoft Corporation – Imagery © NASA).

The Kalahari is a semi-arid, mostly flat, desert region with an average altitude of about 1,000 m above sea level and lies within regions of Botswana, Namibia and South Africa. It is characterized by seasonal extremes in temperature and rainfall. During the wet season of December to April, (Wilmsen, 1982). The temperatures during summer generally fluctuate between 20° and 45°C, while in winter they can fall below 0°degrees C. Despite its general aridity, the northern and western regions experience higher annual precipitation and so the vegetation is more dense and less seasonal. Here, the vegetation is mostly composed of deciduous trees, shrubs and grasses adapted to erratic rainfall. During the rainy season, water holes can form in the extensive mud flats causing luxuriant plant growth.

Table 3.3 - List of modern hunter-gatherers specimens used, including information about ethnographic group, tooth type, degree of wear, geographical origin, and repository. Repository: 1) Natural History Museum of London, England; 5) Natural History Museum of Vienna, Austria; 7) Department of Anthropology, University of Vienna, Austria.

Specimen	Group	Tooth	Wear	Locality	Repository
FC 810	Inuit	URM1	3	Greenland	1
FC 826	Inuit	ULM1	2	Greenland	1
FC 833	Inuit	ULM1	3	Greenland	1
FC 833-2	Inuit	ULM2	3	Greenland	1
FC 833-3	Inuit	ULM2	3	Greenland	1
FC 835	Inuit	ULM1	3	Greenland	1
FC 857	Inuit	ULM1	3	Greenland	1
BD 1191	Inuit	URM2	3	Greenland	1
AM10 854	Inuit	ULM1	3	Greenland	1
91-12-18-2	Inuit	ULM1	2	Greenland	1
AM10 838	Vancouver Islanders	ULM2	3	Columbia River	1
AM10 839	Vancouver Islanders	ULM1	3		1
AM10 844	Vancouver Islanders	ULM2	3	Vancouver Isl.	1
AM10 853	Vancouver Islanders	ULM2	2	Vancouver Isl.	1
BD 1201	Vancouver Islanders	ULM1	3	Vancouver Isl.	1
BD 1204	Vancouver Islanders	ULM1	2	Vancouver Isl.	1
BD 1206	Vancouver Islanders	URM2	3	Vancouver Isl.	1
BD 1208	Vancouver Islanders	ULM1	3	Vancouver Isl.	1
BD 1210	Vancouver Islanders	ULM1	2	Vancouver Isl.	1
BD 1211	Vancouver Islanders	ULM2	3	Vancouver Isl.	1
FC 838	Vancouver Islanders	URM2	2	Columbia River	1
FC 840	Vancouver Islanders	URM1	3	Columbia River	1
FC 848	Vancouver Islanders	ULM2	2	Columbia River	1
FC 855	Vancouver Islanders	ULM2	3	Columbia River	1
1911-11-14-2	Vancouver Islanders	ULM2	2		1
AM80 968	Fuegians	ULM1	3	Tierra del Fuego	1
FC 1025	Fuegians	ULM1	3	Tierra del Fuego	1
FC 1025-7	Fuegians	ULM1	3	Tierra del Fuego	1
2-9-18-1	Fuegians	ULM2	3	Tierra del Fuego	1
NHMW 6034	Fuegians	ULM2	3	Tierra del Fuego	5
NHMW 6035	Fuegians	ULM2	3	Tierra del Fuego	5
NHMW 15353	Fuegians	URM1	3	Tierra del Fuego	5
BRE 87	Australian aborigines	ULM2	3	Australia	5
NHMW 811	Australian aborigines	ULM1	3	Australia	5
NHMW 8687	Australian aborigines	ULM2	3	Australia	5
S1	Bushmen	ULM2	3	South Africa	7
S5	Bushmen	ULM2	3	South Africa	7
S7	Bushmen	ULM2	2	South Africa	7
S9	Bushmen	ULM2	3	South Africa	7
S16	Bushmen	ULM1	3	South Africa	7
S17	Bushmen	ULM2	3	South Africa	7
S19	Bushmen	ULM1	3	South Africa	7

More than 150 species of plants and 100 species of animals were known to be exploited as foodstuffs by the Bushmen (Sahlins, 1968).They typically gather roots, berries, fruits, melons, nuts, leafy greens and edible gums (Lee, 1978). Game taken mainly consists of wildebeest, gemsbok and giraffes. They also hunt birds and reptiles, occasionally collecting honey when available. The animal food component is scarce and unpredictable, rendering meat as only of secondary dietary importance (Lee, 1978). Therefore, the consumption of plant foods normally constitutes between 60 and 80% of the diet (Lee, 1973; Lee & De Vore, 1976; Silberbauer, 1981).

Specific information on this collection is lacking and it also includes individuals from neighbouring populations of Hottentots, Bantus and Hereros (Benton, 1965), which have pastoral and agricultural economies. Specimens S1 and S16 are Bushmen, while S5, S7, S9, S17, and S19 belong to the Hottentots and in particular to the Korana tribe which lived south of the River Orange in the Cape Province (Barnard, 1992) (Fig. 3.7).

Repository: Department of Anthropology, University of Vienna, Austria.

Fuegians

The sample consists of seven specimens belonging to different tribes from Tierra del Fuego. The Fuegian Archipelago is situated in the southern extreme of South America, is divided politically between Chile and Argentina and separated from the mainland by the Straits of Magellan. The territory of Tierra del Fuego is quite mountainous with peaks surpassing elevations of 2,000 m. The climate is characterized by short summers where the average temperature is around 10°C, while the winters are long and wet with temperatures 0°C. The northeastern areas experience strong winds and low precipitation, whereas the southwestern areas are wet, foggy and windy most of the year. Only 30% of the Fuegian Archipelago is covered by forests which are distributed along the slopes of the mountains in the southern and western part. In the north-east areas, the vegetation is scarce and mainly composed of moor. The southernmost islands are characterized by a subantarctic climate where there is no tree cover and the vegetation is primarily composed of shrubs and tundra-type vegetation.

The Fuegians subsistence was based mostly on the consumption of animal protein. The orginal tribes are considered to be functionally extinct as definable ethnic groups(e.g. García-Bour et al., 2004). The Fuegians were divided into four distinct groups each with his own language and customs: the Alcaloof, the Yahgan, the Ona and the Aush (Furlong, 1917; Bridges, 1948) (Fig. 3.8).

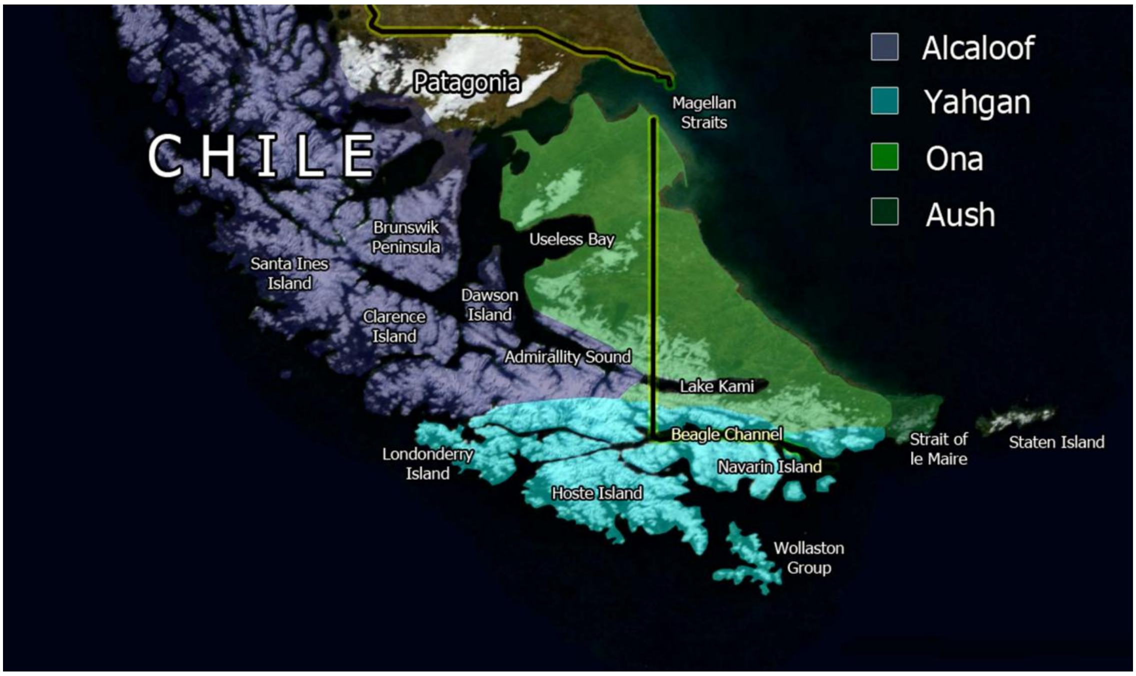


Figure 3.8 - Map of southernmost Patagonia, the Strait of Magellan and Tierra del Fuego, showing the distribution of Fuegian tribes (modified from Furlong, 1917). Map modified from © 2009 Microsoft Corporation – Imagery © NASA.

The Alcaloof inhabited the western part of the archipelago. The Ona occupied the forests of the northern and eastern part of the main island ending their southern range along Lake Kami. This constituted a natural barrier between them and the Yahgan tribe whose territory extended from Desolation Bay through the southern islands as far south as Cape Horn (Bridges, 1948). The Aush (or Eastern Ona) lived on the south-eastern tip of the main island. The diet of the Yahgan and the Alcaloof was mainly composed of fish, shellfish, crabs, birds and seals. In addition, the Yahgans were also known to collect edible berries (Bridges, 1948). The Ona and the Aush lived almost entirely on guanaco meat, occasionally hunting birds and exploiting stranded whales (Bridges, 1948). Not much information is available for the individual specimens themselves. The specimen AM80 968 is an adolescent female coming from Philip Bay which is located on the northern cost of the main island of Tierra del Fuego and therefore she probably belonged to the Ona tribe as is the specimen NHMW 6035. The specimen NHMW 6034 belongs to the Alcaloof and NHMW 15353 comes from Patagonia (the Chubut region) and is therfore likley a Tehuelche.

Repository: Natural History Museum of Vienna, Austria (NHMW 6034, NHMW 6035 and NHMW 15353).
Natural History Museum of London, England (AM80 968, FC 1025, FC 1025-7, and 2-9-18-1).

Vancouver Islanders

Fifteen specimens come from Vancouver Island and the territories situated along the Columbia River (Fig. 3.9). The climate is maritime and characterized by cool summers, wet, mild winters and dominated by temperate rainforest (Ames & Maschner, 1999). In the southern part, along the costal lowland of Washington and Oregon State, the vegetation becomes more open with the formation of grasslands and prairies (Ames & Maschner, 1999).

Figure 3.9 - Map of Northwestern Coast occupied by Native Americans tribes (modified from © 2009 Microsoft Corporation – Imagery © NASA).

The subsistence of these populations was mainly based on the exploitation of animal proteins. The coastal plains were rich in neritic fauna including a great variety of fish, shellfish (crustaceans, molluscs), birds and sea mammals. In addition, beached dolphins and whales were exploited when possible. The molluscs were steamed and often smoked and preserved (Ames & Maschner, 1999). However, their subsistence economy was based mostly on the exploitation of salmon which were abundant and available at predictable times and places

(Ames & Maschner, 1999). They were consumed fresh with the remainder dried, smoked and stored. Terrestrial mammals such as deer, elk and wild goat were also hunted. Plant foods were more important in the southern areas than in the north. Berries, ferns, bracken, acorns and hazelnuts were also collected when available were to supplement the winter diet (Ames & Maschner, 1999). Roots and corms were also made into flour.

Repository: Natural History Museum of London, England.

Inuit

This sample is composed of ten specimens with a rather heterogeneous distribution and includes individuals from the western coast of Greenland, the northern islands of the Nunavut region (Canada) and the Seward Peninsula of western Alaska (Fig. 3.9).

These regions are characterized by a maritime arctic climate with short, mild summers (mean temperatures ~10°C), and cold, long, stormy winters. The annual precipitation is generally low (between 60 and 125 mm/ yr) and largely of snowfall. Plant growth is limited by permafrost and so the ecozone is dominated by low tundra mosses and lichens.

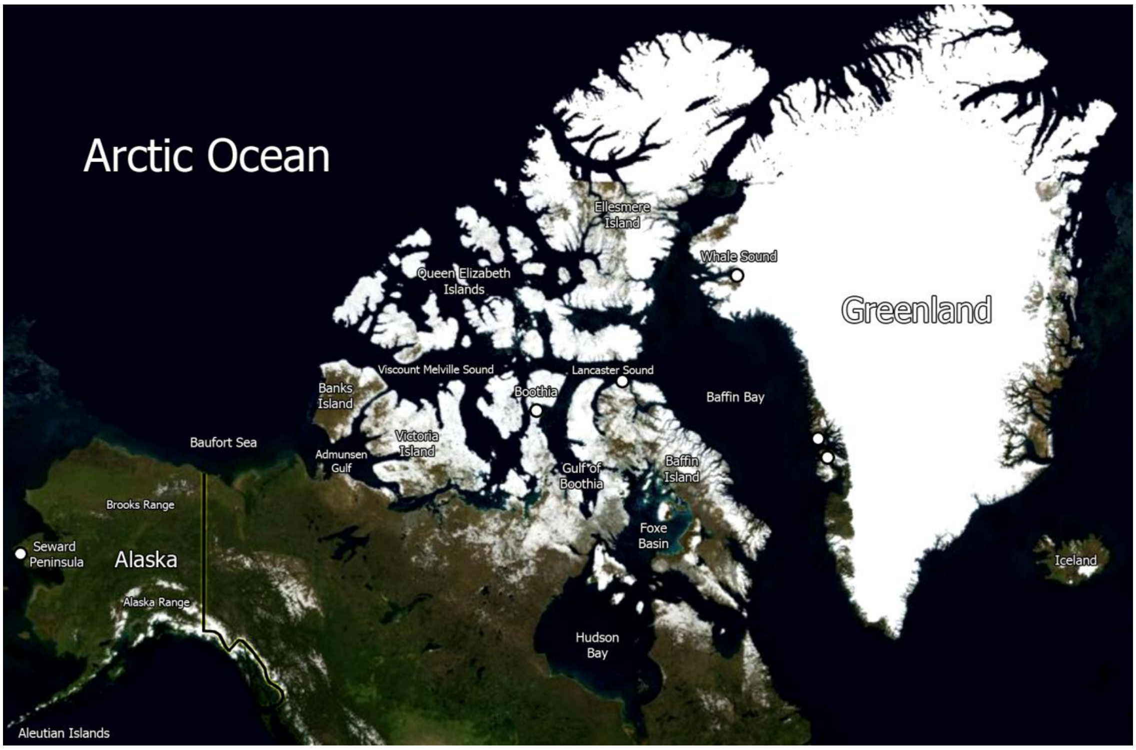


Figure 3.10 - Map of the Arctic territory indicating some of the Inuit specimens (in circle) included in this analysis (modified from © 2009 Microsoft Corporation – Imagery © NASA).

The Inuit diet is almost entirely composed of animal protein. The Inuit living north of Hudson Bay and west of Baffin Bay, mainly base their winter diet on seals, eating all parts of the animal including the blood (Sinclair, 1952). In spring, they subsist primarily on walrus meat while occasionally hunting polar bears and musk ox. In summer, they rely more on terrestrial animals especially caribou but also include fish (especially salmon), birds (ducks and geese) and vegetable materials such as berries, roots and some algae although the consumption of plant foods is not large (Sinclair, 1952).

The Ipiutak, from the Alaskan west coast, have similar diet hunting sea mammals (seals and walrus) in addition to caribou (Lester & Shapiro, 1978; El Zaatari, 2007). Inuit from the Greenland west coast primarily exploit aquatic animal food sources due to the disappearance of caribou and musk ox (Heinbecker, 1928). They subsist mainly on seal meat but also hunt other animals such as walrus, narwhal, beluga, polar bear and arctic hare (Heinbecker, 1928). In addition, they exploit birds and their eggs which are seasonally numerous and easily accessible (Heinbecker, 1928; Gotfredsen, 1997). The Inuit often eat their food raw but sometimes frozen or dried (Sinclair, 1952). De Poncis (1941) and Balikci (1970) reported the chewing of seal skin for prolonged periods of time.

Specimen FC 826 comes from Whale Sound, located west of Qaanaaq in north-western Greenland. The specimens FC 832-2 and FC 833-3 come from the southern-western Greenland coast. The specimens FC 810 and FC 857 are from Greenland but no more specific information is available. Specimen FC 833 comes from Lancaster Sound, north of Baffin Island while FC835 is from the Boothia Peninsula west of Baffin Island. Lastly, specimen BD 1191 comes from Port Clearance situated along the Seward Peninsula on the Alaskan west coast and therefore probably belongs to the Ipiutak.

Repository: Natural History Museum of London, England.

Australian aborigines

The Aborigines inhabited the entire Australian continent under various geographic and climatic conditions ranging from the northern tropical coastal regions through the central deserts to the cool, temperate southern regions (O'Dea, 1991) (Fig. 3.11).

They were omnivorous but generally able to secure large quantities of animal protein (Brand-Miller & Holt, 1998). The diet composition and the relative proportion of plant and animal foods was greatly influenced by seasonal changes and geographic location (O'Dea, 1991).

Animal protein was composed of mammals, reptiles, birds, shellfish and insects. Almost every edible part of the animal was consumed including muscles, fat deposits and internal organs (O'Dea, 1991). They exploited a variety of plant foods including tuberous roots, seeds, fruits, berries, nuts, beans and honey. Food was generally cooked by roasting on coals or baking in an earthen oven (O'Dea, 1991). Sometimes it was dried and stored. Many plant foods were simply eaten fresh (O'Dea, 1991).

The sample is composed of 3 specimens. The only information available is for specimen NHMW 87 which comes from Ardrossan, a coastal area 150 km northwest of Adelaide (Fig. 3.11).

Repository: Natural History Museum of Vienna, Austria.

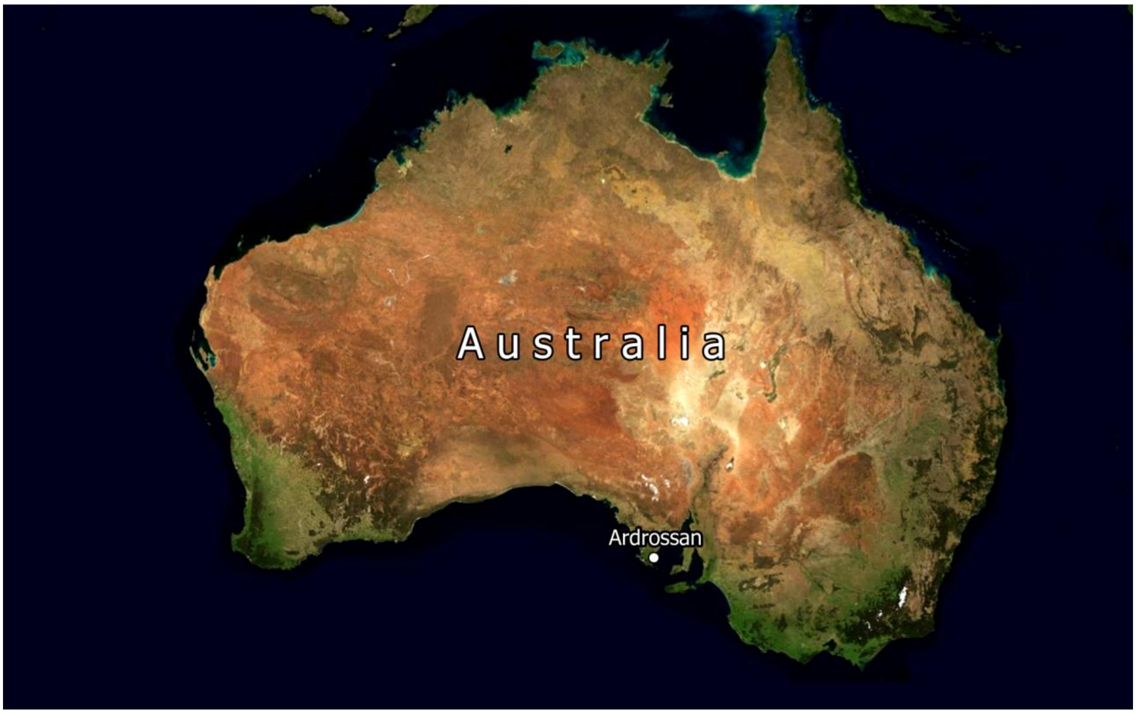


Figure 3.11 - Map of the Australian continent, illustrating the location of one Australian aborigine specimen (in circle) included in the study (modified from © 2009 Microsoft Corporation – Imagery © NASA).

Chapter 4

Methods

4.1 Wear Facet Terminology Used

Wear facets were defined on the occlusal tooth surface following the terminology of Maier & Schneck (1981), which identified a maximum 13 pair of facets in hominoid molars (Fig. 4.1).

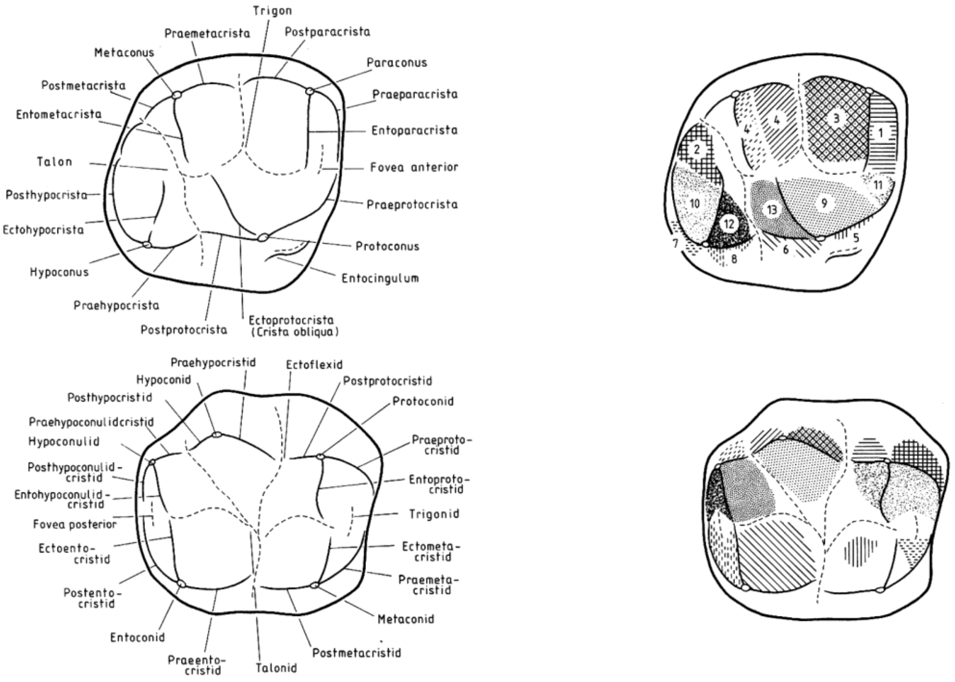


Figure 4.1 - Occlusal wear facet terminology used by Maier & Schneck (1981).

In addition, using the dental occlusal concept (Douglass & DeVreugd, 1997; Schulz 2003; Schulz & Winzen, 2004; Kullmer et al., 2004; Kullmer et al., in press; Ulhaas et al., 2007) the wear facets were divided and grouped according to the possible three-dimensional occlusal movements responsible for their formation starting from a position of maximum intercuspation (Fig. 2.7). The facets 1, 4, 5 and 8 are in contact during lateroretrusive movements (LRT). Facets 2, 3, 6 and 7 are produced in lateroprotrusion (LPT) while facets 9, 10 and 12 are in contact during mediotrusion (MT) and immediate side shift (ISS). Lastly, facets 11 and 13 correspond to medioprotrusion (MPT).

The different occlusal movements and the corresponding wear facets are identified using a colour coding system: blue for lateroretrusion, yellow for lateroprotrusion, green for mediotrusion + immediate side shift, and orange for medioprotrusion.

Depending upon the occlusal relationship and/or the complexity of the occlusal grooves and dentin exposures, wear facets could be divided and/or be in contact with two opposing occlusal areas simultaneously. In this case we adopted a modified labelling system splitting homologous facets into two or more parts.

For example, facet 4' from the Mayer & Schnek system (1981) can be in occlusion at the same time as facet 2, thus corresponding to the same lateroprotrusive movements. Therefore, in certain instances, facet 4' can be subdivided and renamed facet 2.1 (Kullmer et al., 2009).

We also recognized flat, worn areas on the tips of the four main upper molar cusps. These features have been named 'tip crush areas' and are believed to be produced during puncture-crushing where the maxillary cusps occlude with the basins of the mandibular molars (Gordon, 1984; Janis, 1990).

4.2 Creation of 3D Digital Models

In order to generate virtual three-dimensional models of teeth, dental casts were digitized using a white-light scanning system (smartSCAN 3D, Breuckmann GmbH).

4.2.1 Scanning

The smartSCAN 3D (Breuckmann, GmbH) is a white-light scanning system composed of a grid projector and two CCD cameras (1384 x 1036 pixels) (Fig. 4.2). The projector transmits a ray of light with a grid pattern which strikes the object from a known position in a known direction. The grid pattern projected on the object is recorded by the two CCD cameras which produce a three-dimensional point cloud with an x-y resolution of 55µm. In order to generate a virtual 3D model of the whole object, the specimen is scanned from different views. The different views are obtained by moving the tripod mounted scanner around the object.

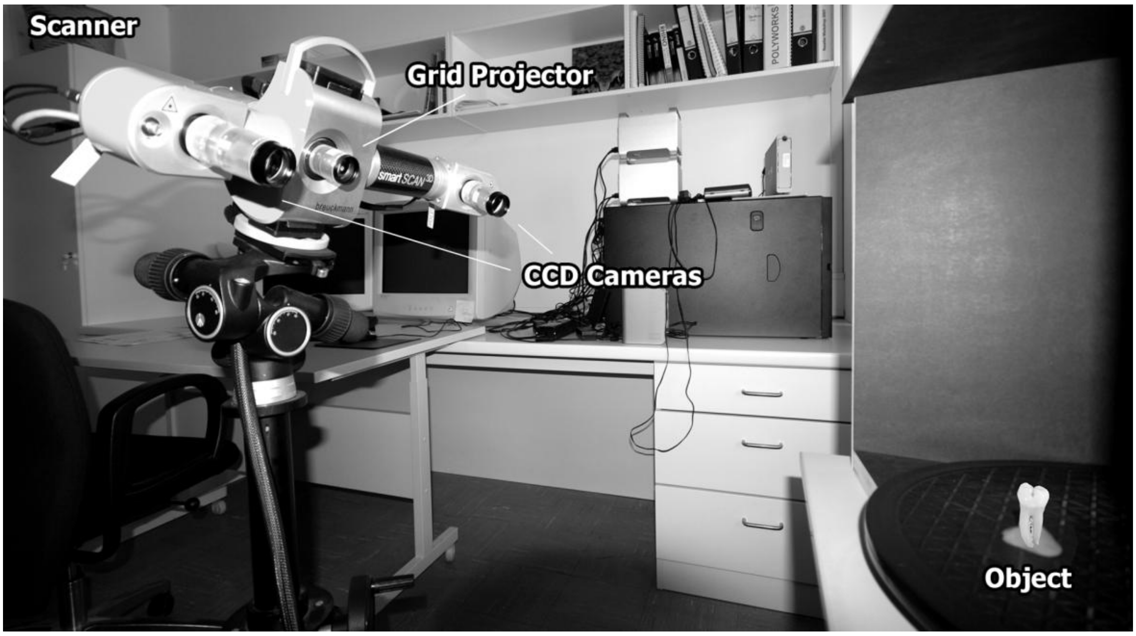


Figure 4.2 - SmartSCAN 3D (Breuckmann, GmbH).

The number of views needed depends on surface reflection and complexity of the object (Ulhaas et al., 2007). Tooth enamel, has quite reflective and transparent properties which prevents the accurate capture of surface information directly from the original tooth.

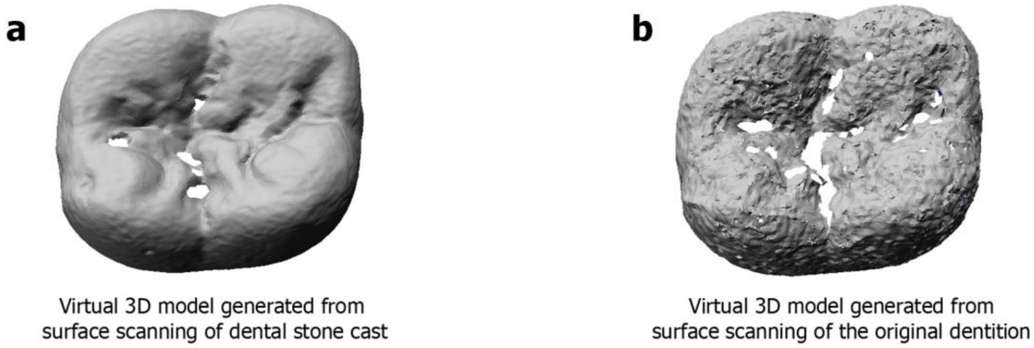


Figure 4.3 - Polygonal 3D model generated from surface scanning of dental stone cast (a) and original dentition (b).

Teeth can be coated with talcum powder or ammonium chloride in order to create a matt, opaque surface which is suitable for scanning. However, the particle size and difficult removal of these substances (and others such as Standard-Check Medium Nr. 3 Entwickler spray (Helling, GmbH)) is such that it will fill in micro-features thus limiting the future usability and information viability of specimens. In order to solve this problem, casts were produced from the original dentition using a special non-reflective gypsum (Everest® Rock, KaVo), which allowed the teeth to be scanned more quickly and producing higher resolution models than those from original dentition (Fiorenza et al., 2009) (Fig. 4.3).

4.2.2 Casting

It is important to properly clean dental surfaces before applying impression materials because they are often contaminated by dust or other materials such as glue or varnish. The dental surface was gently cleaned using cotton buds soaked in acetone (Ungar, 1996; Merceron et al., 2004). Afterwards the specimen was moulded using a monophasic technique with a light viscosity polyvinylsiloxane silicone (Teaford & Oyen, 1989; Ungar, 1996; Merceron *et al.*, 2004). The silicone used, Provil® Novo Light C.D.2 (Heraeus Kulzer GmbH), is contained in a cartridge containing two separate components, the base and the catalyst which are automatically mixed through a dispenser gun. To avoid the formation of air bubbles, the impression material was dispensed slowly with the mixing tip constantly in contact with the dental surface. In order to extend the life-span of the mould, once the first layer was laid on the teeth, an additional layer was added to increase the thickness and durability of the mould (Fiorenza et al., 2009).

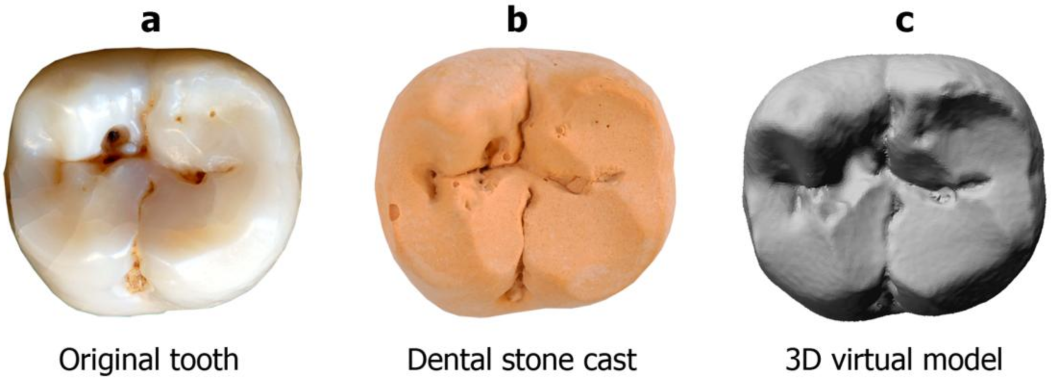


Figure 4.4 - Generation of 3D polygonal model: a) original tooth; b) dental stone cast; c) 3D virtual model.

For each specimen, two types of dental casts were produced. Gypsum casts as described above were first made and then higher resolution casts were produced (Fig. 4.4). The second type was made, in order to be able to identify the occlusal wear facets more precisely (Fig. 4.13). This was accomplished using an epoxy composed of the resin Larit L-160 and the hardener

Larit 502 (Lange und Ritter, GmbH). Since the epoxy is a transparent material, a matt-black colouring paste was added to the resin and blended to produce a homogeneous mix (Fiorenza et al., 2009).

4.2.3 Post-processing of the digital model

Collection and alignment of the scan-data point clouds was carried out using optoCAT software (Breuckmann, GmbH). Different views acquired with the surface scanner were manually aligned by selecting three homologous points on each image and then instructing the system to compute a best fit alignment using a maximum point distance of 0.5 mm, until a sub-sampling ratio of 1/1 was reached (Fig. 4.5).

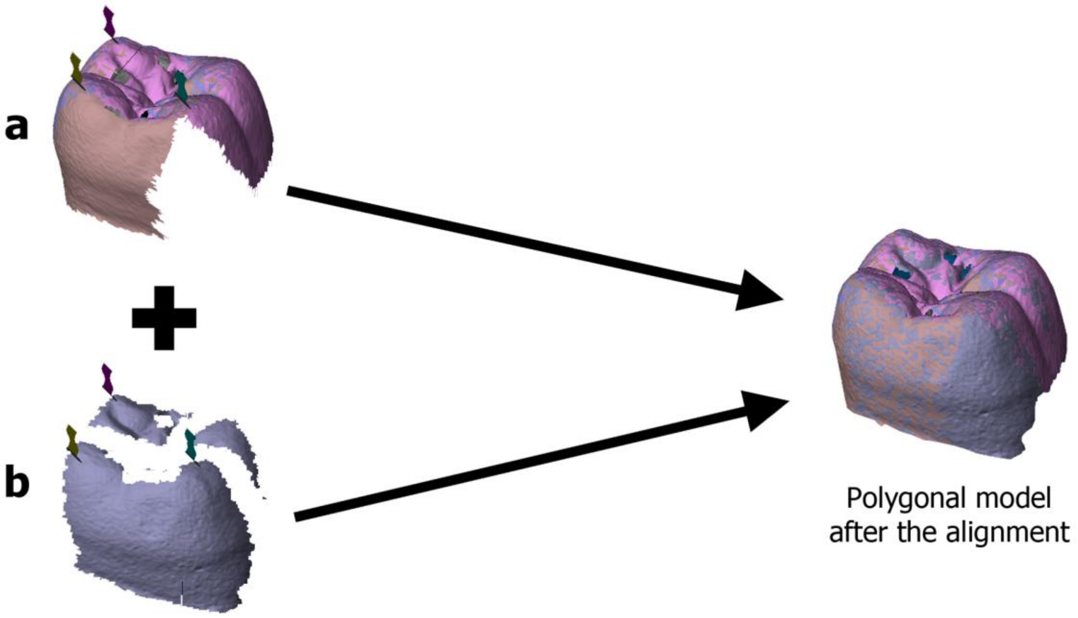


Figure 4.5 - Alignment of the scan-data.

The finalized 3D models were then saved in *.STL file format (Fig. 4.7). A detailed surface scanning tutorial using optoCAT software v. 2007 (Breuckmann, GmbH) is included in the Appendix A.

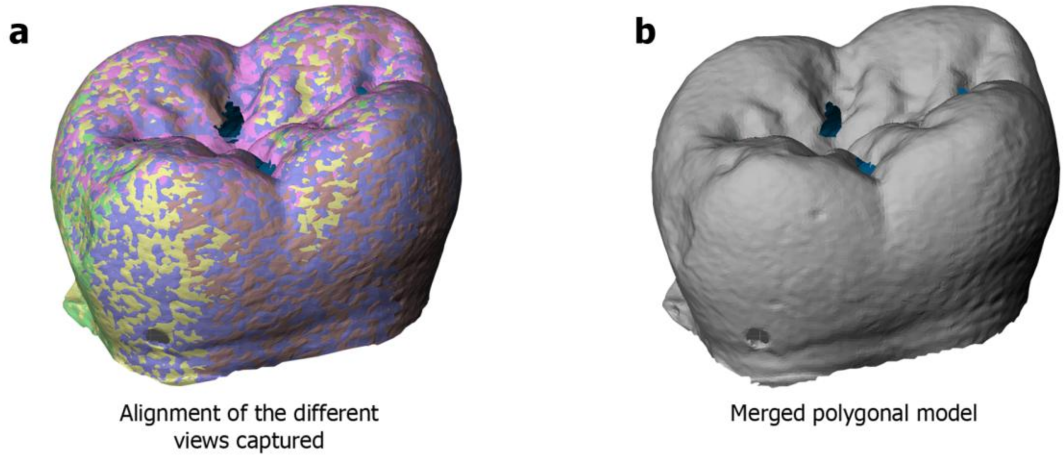


Figure 4.6 - Final alignment (a) and merging (b) of the scan-data.

The 3D virtual models were further post-processed using PolyWorks® 10.1 (InnovMetric Software Inc.), a 3D model editing software package. The rough polygonal model was imported into the IMEdit module where stray or aberrant digital triangles and/or vertices were manually identified and removed.

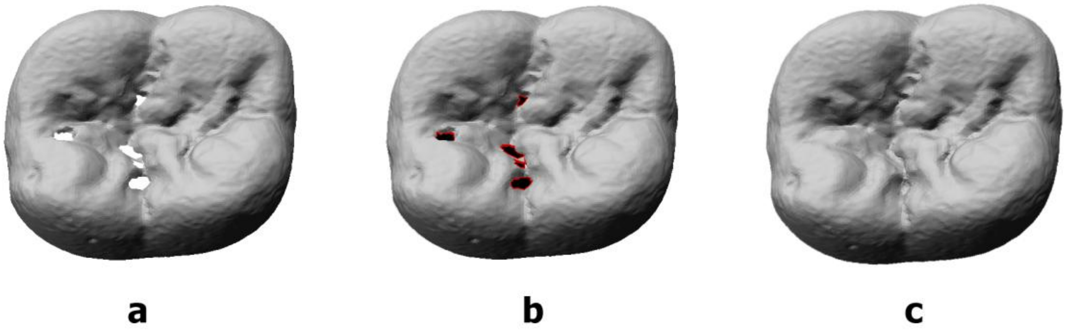


Figure 4.7 - Polygonal model filling system: a) 3D virtual model showing different holes; b) identification and automatic outlining of polygonal holes; c) filling process.

The complexity of the object being scanned can greatly affect the final 3D models external competency. In general, the higher more variable the topographic relief of the object being scanned, the less complete the final scan will be as minute shadows will be left on the polygonal model (seen by the system as holes) where the gridded light beam was not able to penetrate (i.e. 'hills' produce shadows/ holes in 'valleys'). These holes are automatically identified by the editing system and filled using a shape following algorithm (Fig. 4.7).

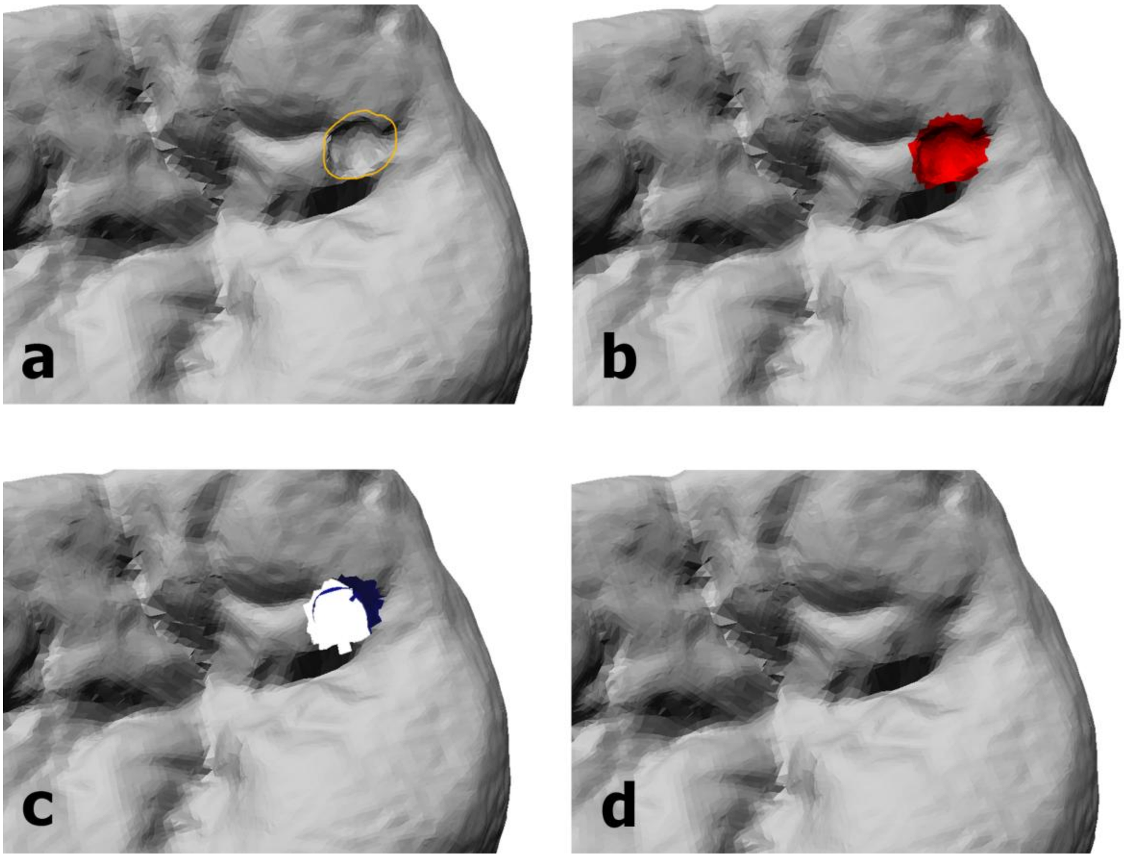


Figure 4.8 - Air bubble removal from a 3D polygonal model: a) air bubble identification; b) air bubble manual outlining; c) clearing the air bubble polygonal surface; d) filling process.

In a similar fashion, any air bubbles formed during casting can be manually identified, edited out and filled (Fig.4.8).

4.3 Measurements

The three-dimensional digital tooth models generated from surface scanning of dental casts were analyzed using the Occlusal Fingerprint Analysis method (OFA). This technique describes and quantifies occlusal wear pattern based on two angles (dip and dip direction) and the area and perimeters of wear facets (Kullmer et al., 2009). Prior to analyzing the occlusal surface, each polygonal model must be properly oriented.

4.3.1 Orientation

The digital model of each tooth was imported into the IMEdit module of Polyworks® and the cervical margin was manually delimited using the polyline tool (Ulhaas et al., 2004, 2007). A marginal area of 0.2 mm above and below the cervical polyline was defined and a cervical plane was created and inserted by means of the least square, best fit method (Ulhaas et al., 2004, 2007; Kullmer et al., 2009) (Fig. 4.9).

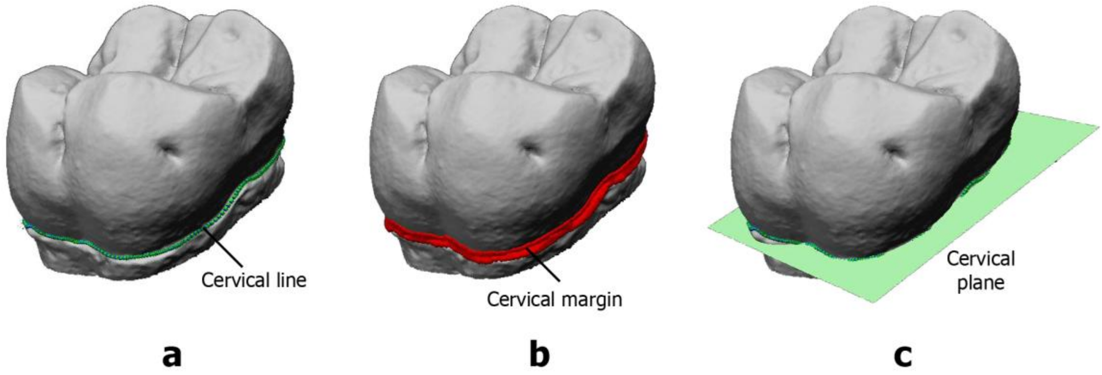


Figure 4.9 - Tooth polygonal model orientation: a) cervical polyline insertion; b) creation of a cervical margin 0.2 mm above and below the cervical line; c) insertion of a best-fit plane (cervical plane) along the cervical margin.

However, the complete cervical margin is visible only in virtual models obtained from isolated teeth. So, in the case of modelled tooth rows, individual molars were virtually cut from each other and then analyzed individually (Fig. 4.10).

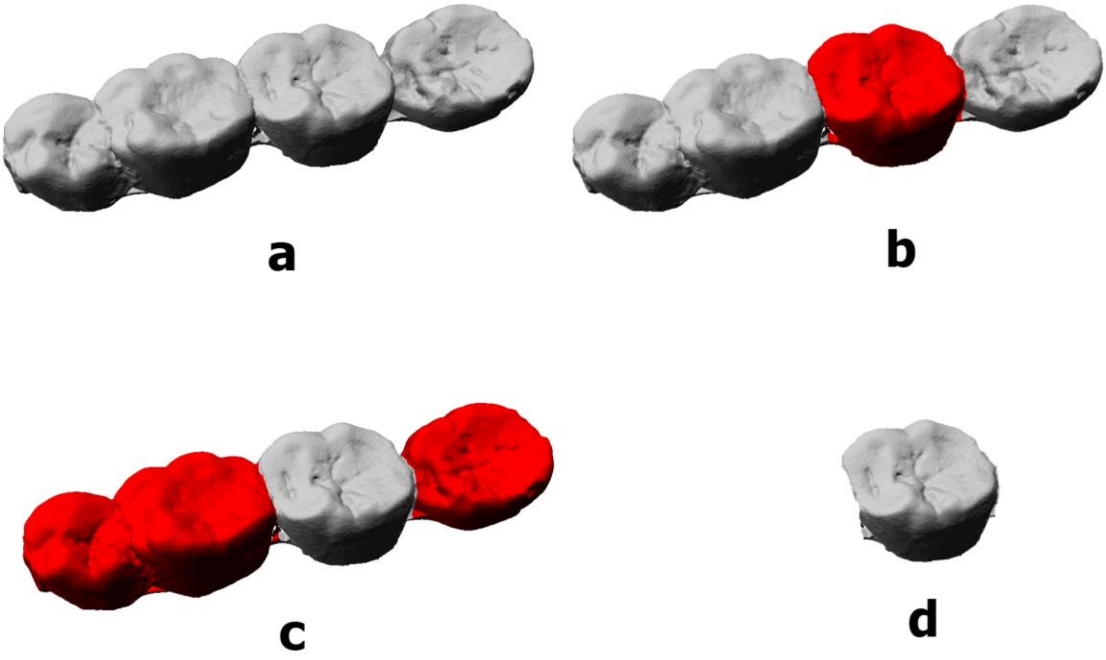


Figure 4.10 - Virtual cut of isolated molars from modelled tooth rows: a) polygonal model of a tooth row; b) isolated molar selection; c) inverse selection; d) virtual detachment of the isolated molar selected.

The cervical line was defined manually on the buccal and lingual sides with the missing mesial and/or distal sides reconstructed virtually using a curve closing tool (Fig. 4.11). Since each polygonal model has its own *xyz* coordinates determined by the objects orientation during surface scanning, it is essential to translate the cervical plane to a standardized *xy* plane (Fig.

4.12a). The Polyworks editing interfaces initially generate a *xyz* coordinate system so the *xy* plane only needs to be defined and emplaced on the coordinate system. The cervical plane (and corresponding polygonal model) is then simply automatically mated to the created *xy* plane with the occlusal surface facing +*z*. . The polygonal model was manually aligned in view +*z*, taking the upper left molars as reference models (the right ones being mirrored), where the mesial side was parallel to the vertical axis of the grid pointing to +*y*, while the lingual side pointed to –*x* (Fig. 4.12b).

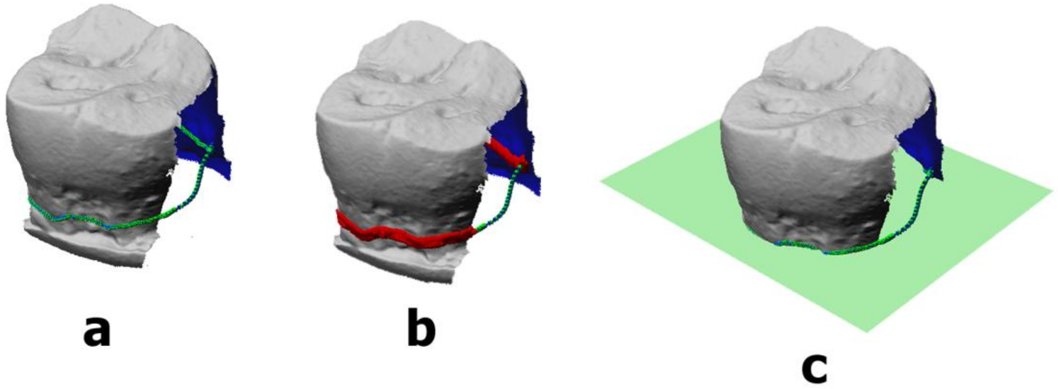


Figure 4.11 - Creation of the reference plane in a virtual detached isolated molar where mesial and distal side are missing: a) polyline insertion along the cervical line; c) creation of a cervical margin; c) insertion of a best-fit plane.

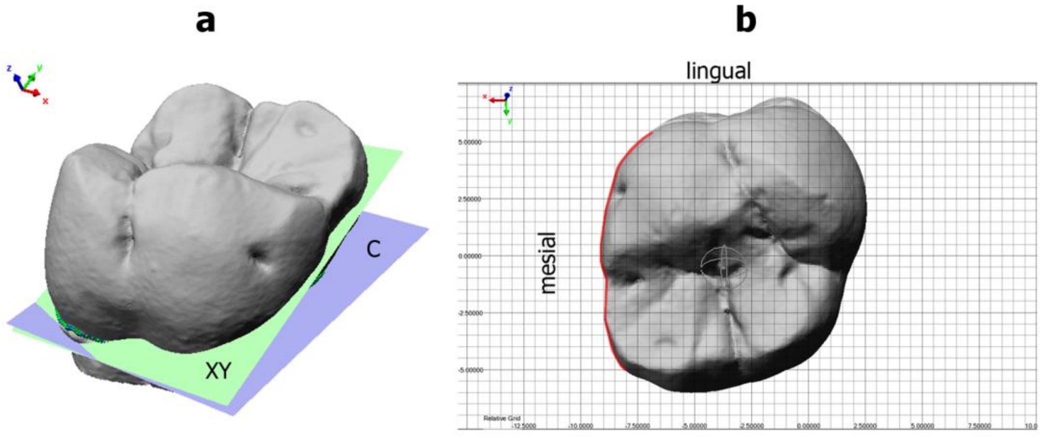


Figure 4.12 - Tooth polygonal model orientation: a) translation of the cervical plane (c) to a standardized *xy* plane; b) manual alignment of the mesial side of the tooth crown (outlined in red) along the vertical +y axis (the lingual side points to –x).

4.3.2 *Wear facet localisation*

Although the polygonal models generated possess a resolution adjusted for wear facet identification, the occlusal surface is actually composed of digitally generated triangles and vertices which do not always absolutely faithfully reproduce the edged and polished surfaces of wear facets. These limiting parameters of resolution and model construction/visualization sometimes rendered the boundary between two facets somewhat indistinct. In order to correct for and control this slight 'melding' of facets, when seeking to mark individual facet areas, the high resolution epoxy casts were always on hand to be examined and so confirm actual facet borders (Fiorenza et al., 2009) (Fig. 4.13).

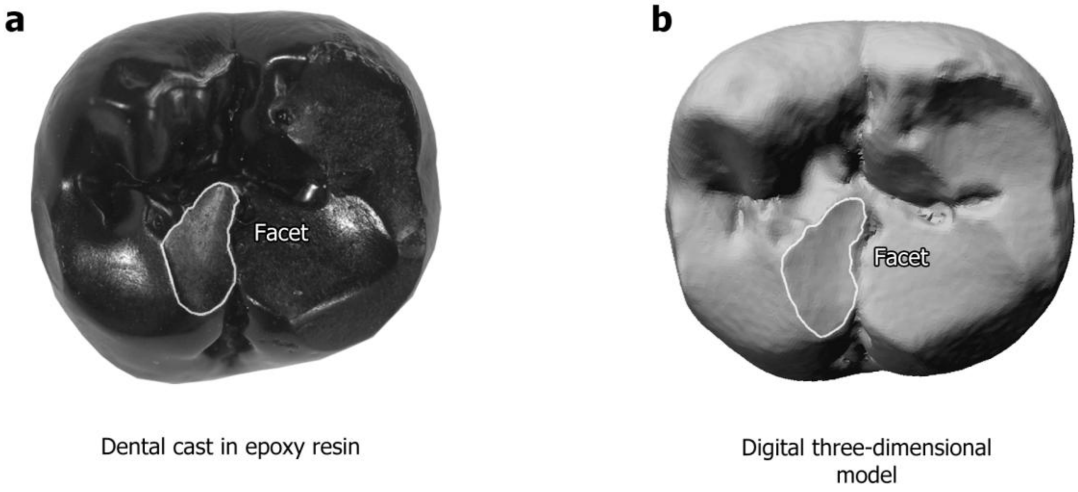


Figure 4.13 - Wear facet localization on a dental epoxy cast (a) and on its corresponding 3D polygonal model (b).

4.3.3 *Area*

For each wear facet, a polyline was inserted manually on the digital model following the anatomical borders of the facet. Next, the triangles included within the facets perimeter were selected and the area in mm^2 was automatically calculated. As larger teeth likely develop larger facets than smaller teeth (both displaying a similar degree of wear), it was necessary to eliminate the size factor and so only relative facet areas were considered. As such, each facet area was divided by the tooth total occlusal area thus correcting for any allometric aberration. In addition, wear facets were grouped in lingual phase I facets (1, 2, 3 and 4), buccal phase I facets (5, 6, 7 and 8) and Phase II facets (9, 10, 11, 12 and 13) which also includes tip crush areas (Janis, 1990) (Fig. 4.14).

4.3.4 Dip and dip direction

Kay & Hiiemae (1974), in order to analyse primate jaw movements from the interaction of occlusal wear facets, adopted and adapted stratigraphic visualization techniques as defined by Lahee (1957).

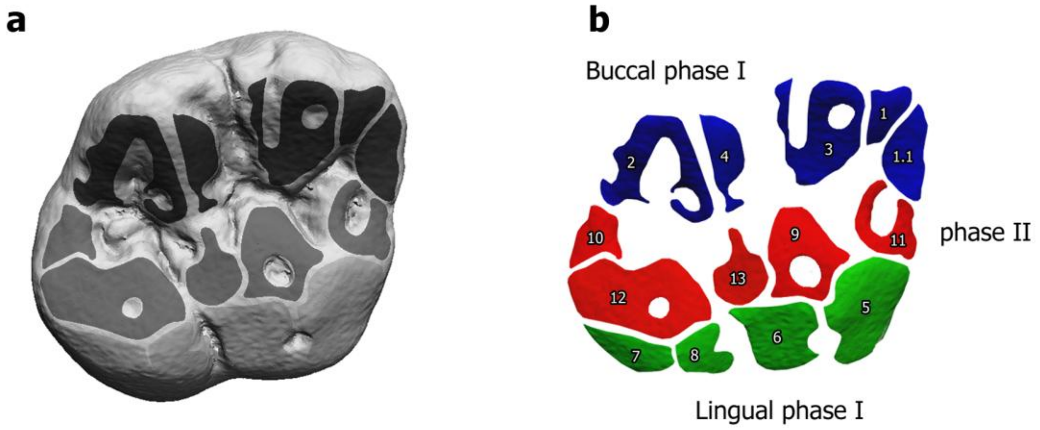


Figure 4.14 - Relative wear facet areas. Tooth polygonal 3D model (a) and wear facets virtually detached (b), divided into buccal phase I facets (blue), lingual phase I facets (green) and phase II facets (red).

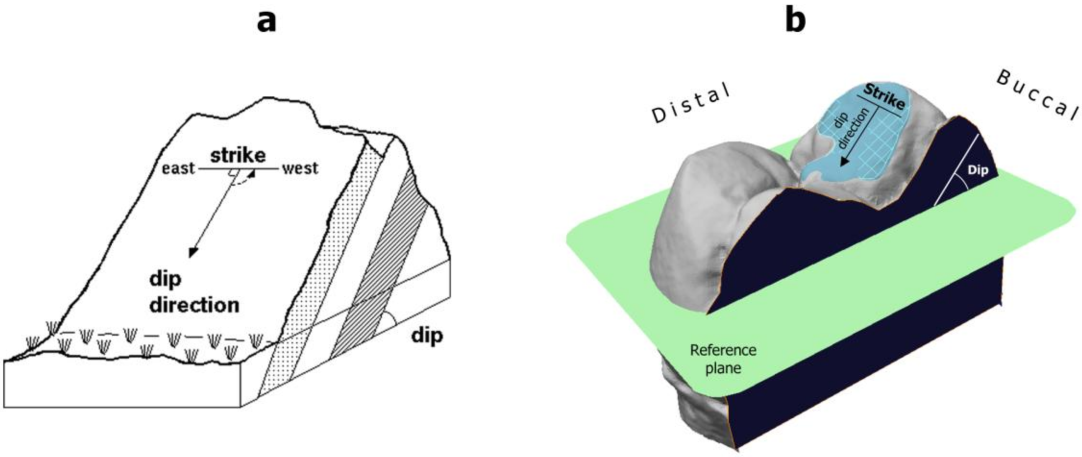


Figure 4.15 – Inclination of planar structure in geology measured by dip, strike or dip directions (a). Dip and dip direction of a wear facet calculated on a 3D tooth polygonal model (b). The picture on the left (a) has been taken from the Earth Science Australia website (http://earthsci.org).

Here, the positions of geologic planes were defined by two angles, "dip" and "strike" (Fig. 4.15). The dip angle represents the planes (facet) inclination as measured in relation to the reference plane. Strike defines the planes horizontal orientation and is measured in relation to the reference planes (tooth crown) longitudinal axis.

However, since strike does not show the direction of occlusal movement, dip direction is used. This is defined as the directions azimuth and is always perpendicular to strike angle. As a reference plane, the cervical plane used to orient the digital model was selected.

4.3.5 Inclination

Dip angle was measured between the facets plane and that of the cervical (Fig. 4.16). In order to create the facet plane, using the IMEdit module of Polyworks, all triangles included in the facets perimeter were selected and a best-fit plane was inserted. Next, these elements were exported to the IMInspect module which automatically computed the facet planes inclination, as it intersected the facet plane and *z* axis.

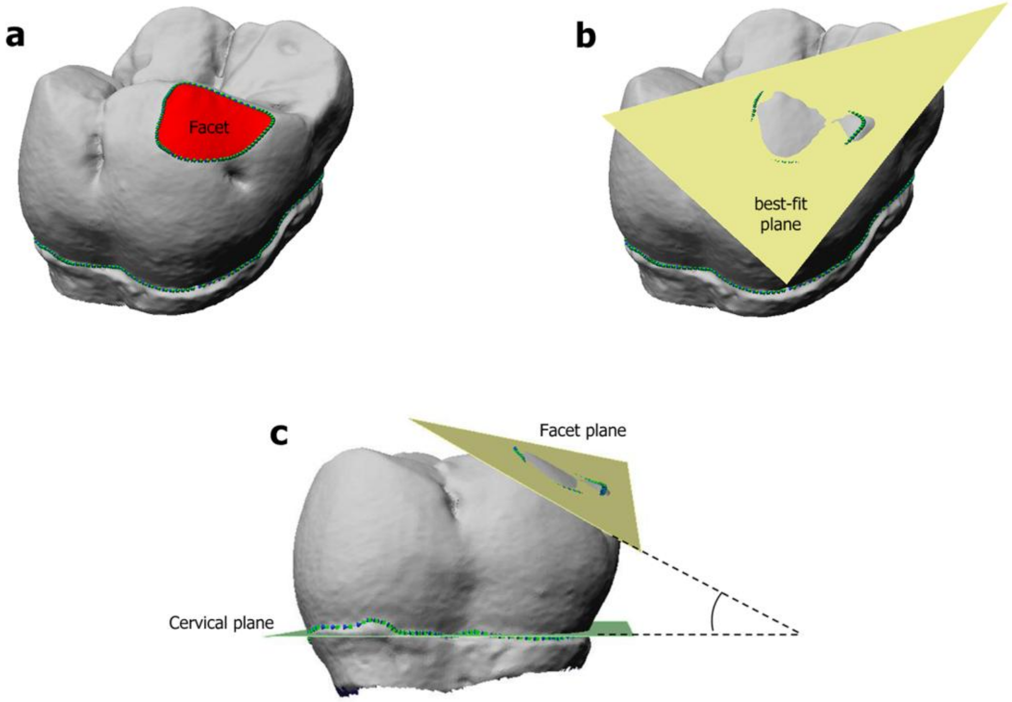


Figure 4.16 - Dip angle measurement: a) selection of all the triangles included within the facet perimeter; b) insertion of a best-fit plane; c) measurement of the angle (dip) between the best-fit plane and the cervical plane.

4.3.6 Dip direction

In order to measure dip direction, the facet outlines and corresponding planes were imported in situ into the IMInspect module. The normal vector for each facet plane was created and then projected onto the cervical plane (Kullmer et al., 2009) (Fig. 4.17a and b). The vectors corresponding to the same mandibular movements were coloured following the colour-code as defined by the dental occlusal compass. Since upper left molars were chosen as the reference model and in order to maintain anatomical orientation for all teeth, the upper right molar vectors were mirrored along the x-z axis. Next, each vector was translated to the coordinate origin (x=0.00; y=0.00; z= 0.00) and vector length was standardized to 10 mm (Kullmer et al., 2009). Finally, a 20 mm diameter circle with its center at the coordinates origin was projected onto the cervical plane. Thus, all facet vectors are enclosed within the circle and pointing in different directions each of which corresponds to different directions of lower jaw movements as schematized by the dental occlusal compass (Fig. 4.17c).

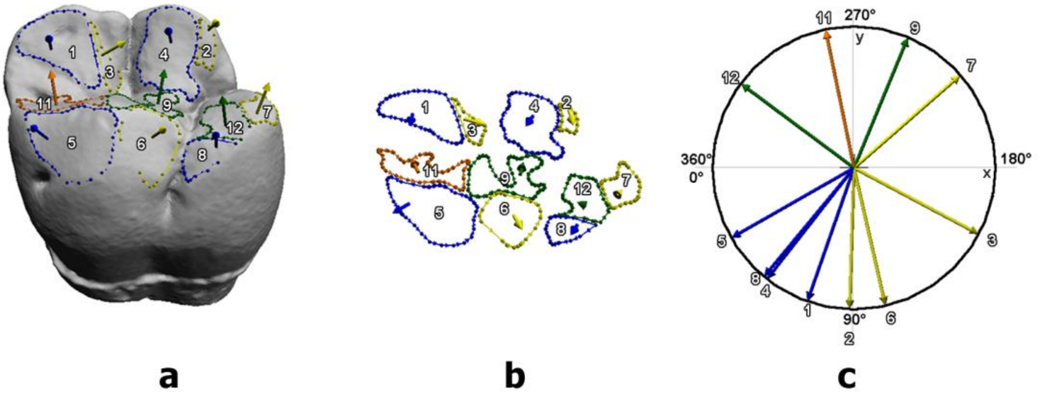


Figure 4.17 - Dip direction measurement: a) tooth polygonal model representing the normal vectors to the wear facet planes; b) projection of wear facet vectors onto the cervical plane; c) numerical editing and translation of each vector, enclosing by a circle (2D occlusal compass).

The intersection between the *x* axis and the mesial point of the circle is defined as origin point (0°). Since the IMInspect module automatically computes the intersection of each vector with the *x-y-z* planes, the dip direction is calculated by subtracting and/or adding the angles value with respect to the *x* and *y* axis in a counter clockwise manner. For instance, the dip direction of facet 12 (Fig. 4.17c) can be calculated by adding to 270° the y axis angle of 53°, or subtracting from 360° the x axis angle of 37°. In both cases we have the same result; 333°.

4.3.7 3D occlusal compass

Although the graphical representation created for calculating dip direction includes two-dimensional information about mandibular occlusal movements for individual teeth, it does not contain information about wear facet inclination.

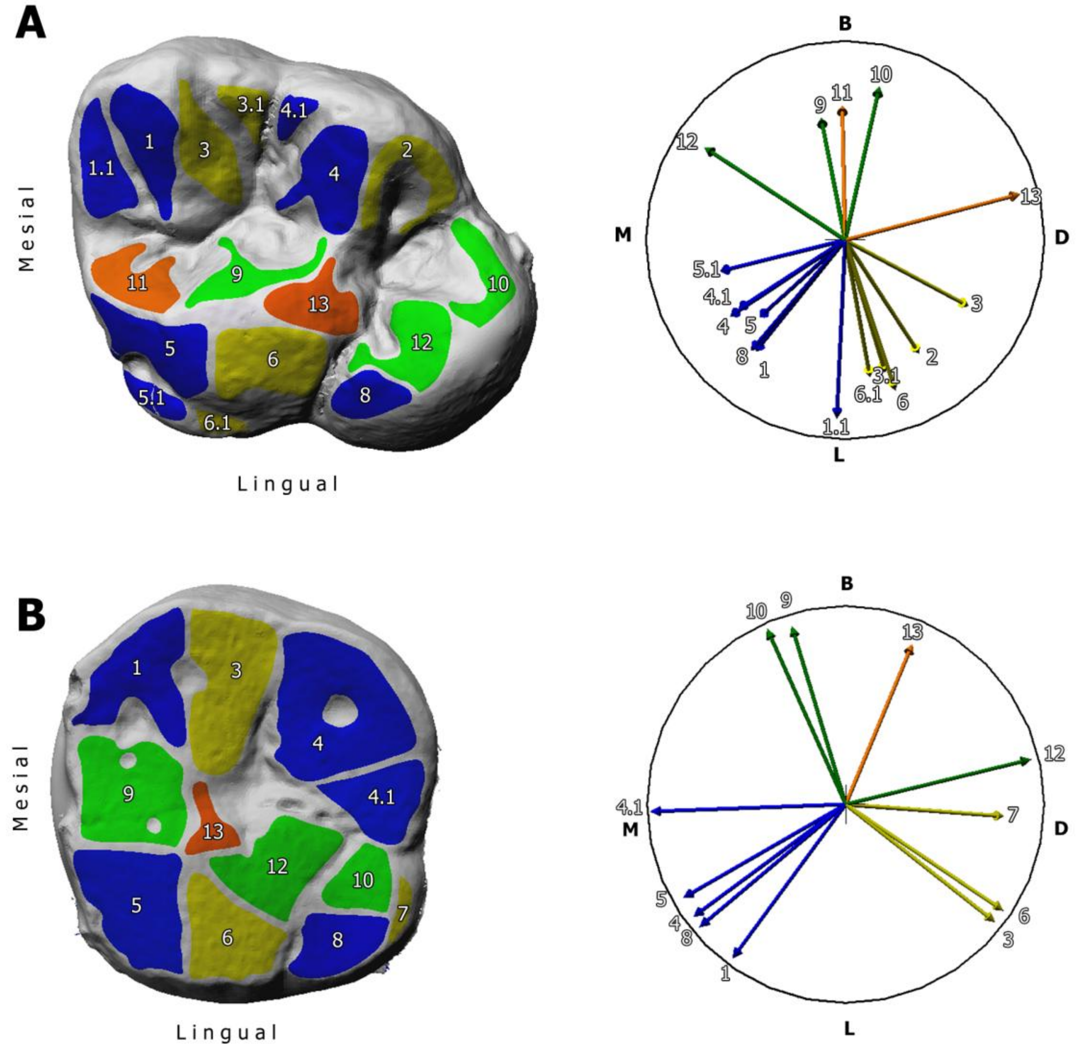


Figure 4.18 - 3D tooth polygonal model and the corresponding 3D occlusal compass of a maxillary molar of a Neanderthal (A) and an Australian aborigine (B). The vector length depicted in the occlusal compass depends on the wear facet inclination. Steep wear facets are represented by short vector lengths (as in A), while flat wear facets are characterized by long vector lengths (as in B).

After projection of the normal vectors onto the cervical plane, it is possible to project each vector onto the facet plane. Thus, each vector is contained in a three-dimensional space describing the dip and dip direction. The 3D graphical schematization represents the individual 3D occlusal compass of each tooth and shows the major directions of contact between the upper and lower dentitions (Kullmer et al., 2009) (Fig.4.18).

4.3.8 3D occlusal relief index

The occlusal relief index was calculated by dividing the 3D surface area into its corresponding 2D base (Kullmer et al., 2002; Ulhaas et al., 2004, 2007). The occlusal plane, which is parallel to the cervical plane, is translated vertically along the *z* axis until it reaches the deepest point of the occlusal surface; the central fossa (Fig. 4.19a).

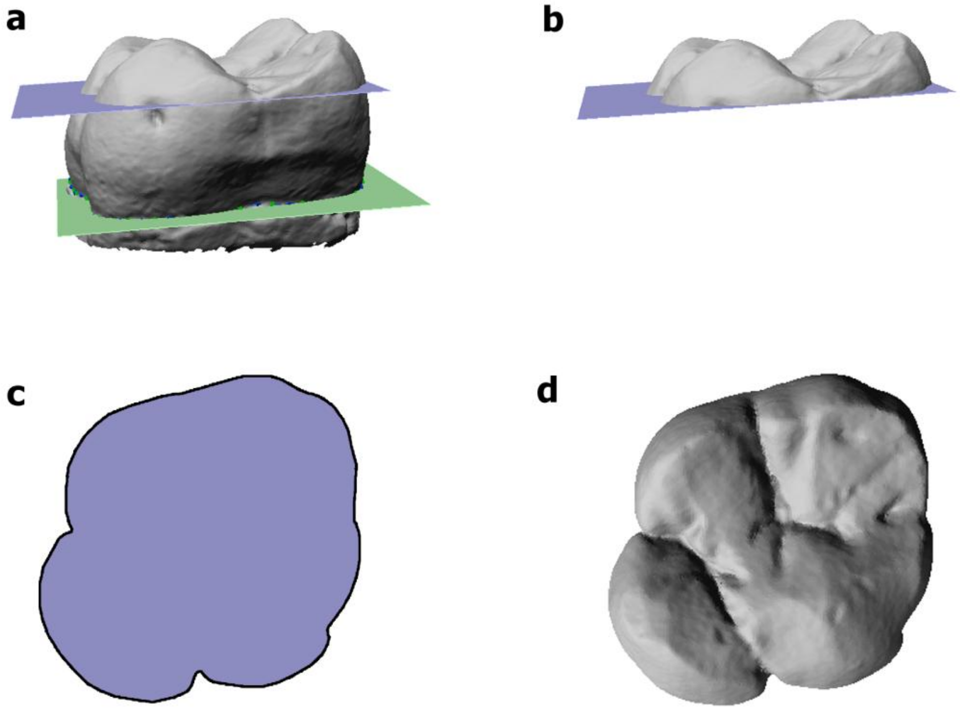


Figure 4.19 - 3D occlusal relief index: a) translation of the cervical plane along the z axis reaching the deepest point of the occlusal surface; b) 3D polygonal model slicing in correspondence of the occlusal plane; c) 2D occlusal area; d) 3D occlusal area.

The occlusal grooves generally converge at the central fossa. However, the upper molar lingual facets (5, 6, 7 and 8) are characterized by high inclination showing steep slopes more apically than the occlusal grooves. In this case, the lingual facets apical limit has been selected as the occlusal surfaces deepest point. Afterwards, the digital model was sliced with respect to the occlusal plane and the 2D area could then be measured (Fig. 4.19b and c). As some molars were digitally detached from the entire tooth row, the distal and/or mesial sides were missing and needed to be virtually reconstructed. The 3D area was then calculated by selecting all the triangles above the occlusal plane (Fig. 4.19d).

A detailed tutorial on how to use the IMEdit and IMInspect modules of PolyWorks® 10.0 (InnovMetric Software Inc.), for obtaining the OFA measurements from digital polygonal models of teeth, is included in the Appendix B.

4.4 Statistical Analysis

Paleontological data are invariably incomplete (Hammer & Harper, 2006). Our fossil sample is rather heterogeneous chronologically and geographically such that it is only possible to identify small groups. An explorative data analysis for each variable (mean and standard deviation) and for each group has been provided. As the presence of a small sample size prevents the assumption of a normal distribution, the statistical comparison has been carried out using non-parametric tests.

For the comparison between two groups, the Mann-Whitney U test valid only for N>7 (PAST) was employed. When the sample size was lower than N>7, the comparative statistical analysis has been carried out using the Permutation t test. In both Mann-Withney U test and Permutation t test, the p values have been corrected with Bonferroni adjustments. Groups of specimen numbers lower than three were not included in the statistical comparison. The proportion of the wear facets were visualized using the ternary plot which visualizes the relative proportion of three variables. Each variable is placed at the apex of a triangle and the sample is plotted as a set of points inside this triangle (Hammer & Harper, 2006). A sample consisting entirely of A will be placed at the corner with A, while a sample consisting of equal proportions of A, B, and C will plot in the center (Hammer & Harper, 2006). A Non-Parametric MANOVA (one-way NPMANOVA) analysis, based on any distance measure (Anderson, 2001), was applied to the multivariate sample composed of three variables (buccal, lingual and phase II facets). Pairwise NPMANOVA comparisons between the three variables have been carried out using a post-hoc test (Bonferroni).

In addition, a Canonical Variates Analysis (CVA) has been used to produce a scatter plot of specimens along the two first canonical axes, producing maximal and second to maximal separation between all groups (multigroup discriminant analysis) (Hammer & Harper, 2006). In one case (ecogeographic variation within the entire fossil sample), a CVA biplot has been produced, showing the projection of the original axes (variables) onto the scattergram.

The strength and direction of the possible linear relationships between two variables were measured using the Pearson Coefficient. In addition, a linear regression was carried out calculating the coefficient of determination which indicates the proportion of variance that can be explained by the linear association (Hammer & Harper, 2006).

The measurement of dip direction represents directional data enclosed in a circular space located between 0° and 360°. Most statistical methods are not directly applicable to directional data because of the cyclical nature of such data (Hammer & Harper, 2006). For instance the difference between a value of 350° and a value of 10° is not 340° but only 20°. In order to evaluate if wear facet dip directions show a preferred orientation or a uniform distribution, the Rayleigh's test (Mardia, 1972; Swan & Sandilands, 1995) has been employed. In addition, the pairwise comparison based on the Watson-Williams test, is used in order to determine if the mean angles between two or more samples differ significantly.

The statistical analysis of the linear and circular data, including the ternary plots, has been computed using the software PAST v.1.83 (PAlaeontological STatistics) (Hammer et al., 2001) and R software (R Development Core Team 2008). All other graphical representations and linear regression analyses were carried out using SPSS software.

Chapter 5

Results

5.1 Wear Facet Identification

The occlusal macro-wear pattern in Neanderthal has never been described in detail. In this chapter an overview of the general occlusal wear pattern in Neanderthal molars, derived from qualitative analysis based mostly on the specimen of Le Moustier 1 is provided. The description takes into account the distribution of the wear facets on the occlusal crown, depending on the morphological features which characterize Neanderthal dentition. New facets have been described and added to the applied labelling system of Maier & Schneck, (1981). Also the 3D occlusal compass following Kullmer et al. (2009) is considered. The dental nomenclature is primarily based on the works of Van Valen (1968), Szalay (1968, 1969) and Kay (1977).

5.2 Neanderthal Occlusal Wear Pattern

The wear facets vary in number, size, and shape depending on the wear stage, absolute cusp number and morphology (Kullmer et al., 2009). The qualitative description of the Neanderthal occlusal wear pattern is based on the upper and lower first right molar of the specimen of Le Moustier 1 which is characterized by an Angle's Class 1 occlusion (Angle, 1899), showing a slight degree of wear (wear stage 2, according to Smith, 1984), where all 13 pairs of facets (Maier & Schneck, 1981) are identifiable, and do not coalesce (Fig 5.1).

Snapshots in occlusal view of digital polygonal models of maxillary molars from the entire fossil sample (Neanderthals and early *Homo sapiens*), showing the wear facets and their corresponding numbering and color-coding (following the occlusal compass concept of Kullmer et al., 2009), have been included in Appendix C.

The buccal phase I facets are characterized by steep surfaces developed along the lingual slopes of the metacone and paracone in the upper molars and along the buccal slopes of the protoconid, hypoconid and hypoconulid in the lowers. Facet 1 is formed in the upper molars corresponding to the mesio-lingual slope of the paracone, in the flat area between the praeparacrista and entoparacrista. The antagonistic mandibular occlusal contact is found on the mesio-buccal slope of the protoconid, buccally to the postprotocristid.

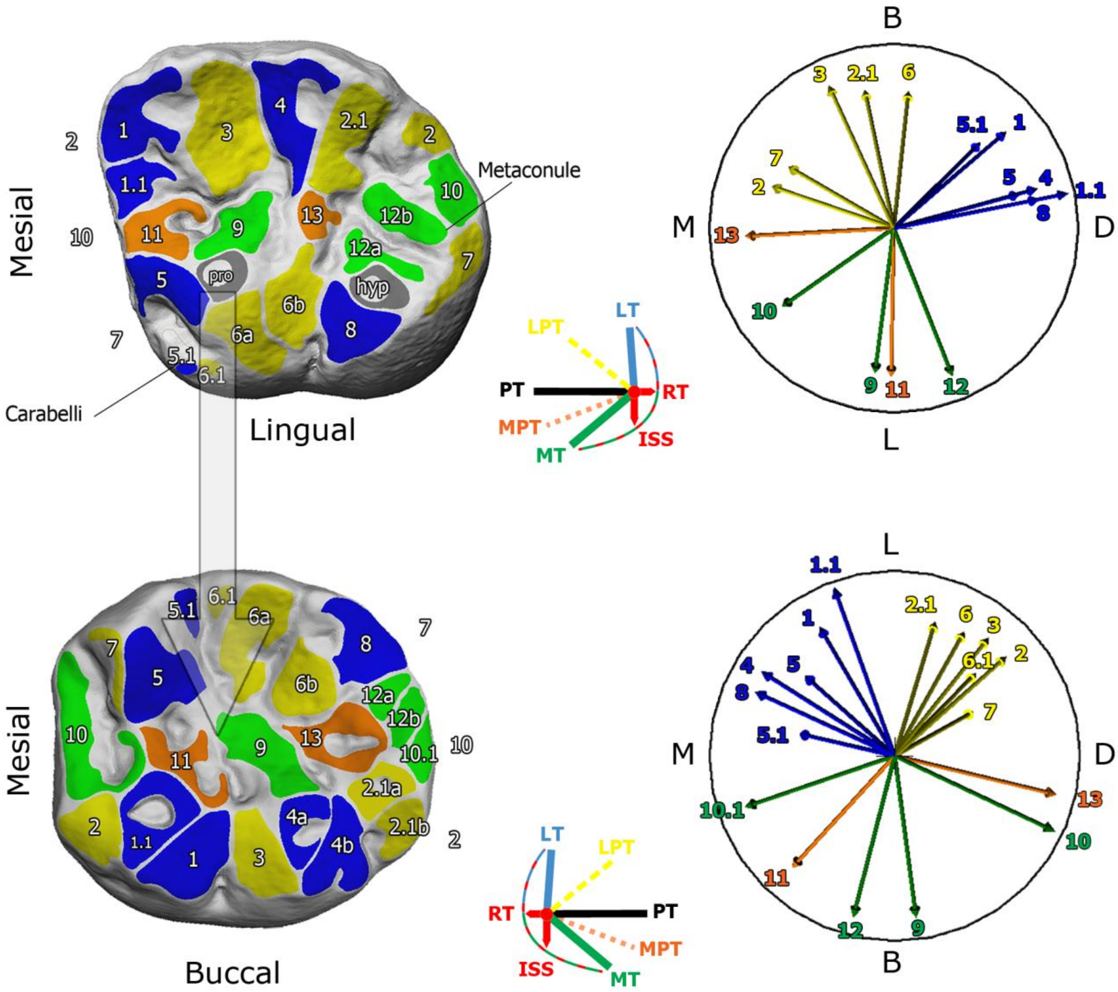


Figure 5.1 - Neanderthal occlusal wear pattern on upper and lower right first molar in the specimen of Le Moustier 1. Wear facets numbering system (1-13) after Kullmer et al. (2009). The division of homologous wear facets in more parts (as facet 4) is pointed out by the letter *a* and *b*. The arrow indicates the occlusal relationship between the protocone of the maxillary molar and the central fossa of the lower during maximum intercuspation. The wear facets identified are color-coded following the dental occlusal concept proposed by Kullmer et al. (2009). Facets 1, 1.1, 4, 5, 5.1 and 8 are in contact during lateroretrusive movements (blue), while facets 2, 2.1, 3, 6, 6.1 and 7 correspond to lateroprotrusion (yellow). Facets 9, 10, 10.1 and 12 coincide with mediotrusion and immediate side shift (green). Finally, facets 11 and 13 correspond to medioprotrusion (orange). On the central part of the figure is illustrated the dental occlusal compass showing major directions of horizontal occlusal movements for upper molars (above) and lower molars (below): laterotrusion (LT), retrusion (RT), lateroprotrusion (LPT), protrusion (PT), medioprotrusion (MPT), mediotrusion (MT), and immediate side shift (ISS). To the right is depicted the 3D occlusal compass scheme (after Kullmer et al., 2009) of Le Moustier 1 (right M^1 above and right M_1 below), where the vectors enclosed by the circle hold information about the inclination (dip angle) and the dip direction of the corresponding occlusal wear facet. B = buccal; L = lingual; M = mesial; D = distal. The original specimen of Le Moustier 1 is housed at the Museum of Prehistory and Early History in Berlin (Germany).

In addition, the maxillary molar shows a further flat facet, labelled as facet 1.1 (facet 1 in the labelling system proposed by Kullmer et al., 2009), displaced mesially to the anterior fovea. This facet occludes with a plateau-like area corresponding to the protoconid, enclosing the dentinal area. Although these contact areas (both in upper and lower molars) are characterized by flat surfaces, and therefore may be considered as crushing wear, they show a slight inclination, corresponding to a lateroretrusive movement, as indicated by the occlusal compass analysis. Facet 2 is the result of the contact between the disto-lingual end of the postmetacrista in the upper first molar and the mesio-buccal slope of the protoconid (buccal to the praeprotocristid) of the second mandibular molar. Facet 2.1 (labelled as 4' by Maier & Schneck, 1981) forms along the disto-lingual slope of the metacone, in the area enclosed between the postmetacrista and the entometacrista on the maxillary M1. It is in contact with the disto-buccal slope of the hypoconulid corresponding to the praehypoconulidcristid.

Facet 3 is localized on the disto-lingual slope of the paracone in the upper molar, occluding with the mesio-buccal slope of the hypoconid in the area buccal to the praehypocristid. Facet 4 forms along the mesio-lingual slope of the metacone, enclosed by the praemetacrista and the entometacrista. The latter occludes with the disto-buccal slope of the hypoconid, corresponding to the buccal side of the posthypocristid.

The lingual phase I facets show contact planes steeper than those of the buccal facets, positioned on the lingual slopes of the protocone and hypocone in the maxillary molars and along the buccal slopes of the metaconid and entoconid in the lower molars. On the mesio-lingual slope of the protocone of the maxillary molar, lingually to the praeprotocrista, a well developed and steep facet 5 is formed, occluding with the mandibular molar between the ectometacristid and the postmetacristid along the disto-buccal slope of the metaconid. Facet 6 develops between the praentocristid and the ectoentocristid along the disto-lingual slope of the protocone in the upper molar. It is situated lingually to the postprotocrista and occluding with the mesio-buccal slope of the entoconid. The Neanderthal first maxillary molars are commonly characterized by the presence of a Carabelli cusp (Bailey, 2002a, 2004, 2006), occluding with the lower molars during the initial stage of wear, determining the formation of one or two wear facets. In the right maxillary M1 of Le Moustier 1 two facets are identifiable on the occlusal surface of the Carabelli cusp, one pointing mesially and the second pointing distally. The mesial Carabelli facet is created during a lateroretrusive occlusal movement, whereas the distal facet develops during lateroprotrusion, as indicated by the directions of facet vectors represented in the dental occlusal compass. Since the mesial and distal Carabelli facets are topographically positioned close to facet 5 and 6, reflecting the same dip directions, they are labelled here as facet 5.1 and facet 6.1 respectively. The Carabelli cusp occludes with the opposing mandibular molar at the lingual groove between metaconid and entoconid, at the area of a C7 cusp, if present. Here, it forms two facets, facet 5.1 on the distal end of the postmetacristid, and facet 6.1 on the mesial end of the praentocristid. However, in maxillary molars possessing a Carabelli cusp, facet 5.1 commonly tends to coalesce with facet 5, while facet 6.1 is less frequent. Facet 7 develops along the disto-lingual slope of the hypocone. It is positioned distally to the posthypocrista and it occludes with the mesio-buccal slope of the metaconid in the area comprised between the ectometacristid and the praemetacristid of the second lower molar. The mesio-lingual slope of the hypocone is characterized by the presence of facet 8, which is in contact with opposing mandibular area located on the disto-buccal slope of the entoconid and enclosed between postentocristid and the ectoentocristid.

The phase II facets show flatter inclination and are formed along the buccal slopes of the protocone and hypocone in the upper molars, and along the lingual slopes of protoconid, hypoconid and hypoconulid in the lower molars. Facet 9 is located on the mesio-lingual slope of the protocone, comprised between the praeprotocrista and the ectoprotocrista (crista obliqua). It occludes with the corresponding mandibular area localized on the buccal slope of the hypoconid, enclosed between the praehypocristid and the posthypocristid. Mesially to the posthypocrista in the upper first right molar of Le Moustier 1, facet 10 is developed along the disto-lingual slope of the metaconule. Facet 10 in the maxillary M1 commonly occludes with the mesio-lingual slope of the protoconid of the second lower molar, while in the lower M1, is usually in contact with the distal side of the upper P4. However, in Le Moustier 1 the right first lower molar shows two facets 10; one is located mesially occluding with the opposing upper P4 (as expected), while the second facet is located distally due to the contact with the disto-lingual slope of the metaconule of the upper M1. Therefore, it has been necessary to define a new label for the distal facet (facet 10.1), maintaining the label of the mesial facet (facet 10). On the mesial end of the praeprotocrista a flat facet 11 develops, occluding with the opposing mandibular molar corresponding to the disto-lingual slope of the protoconid, enclosed between the postprotocristid and the entoprotocristid. Facet 12 forms along the mesio-lingual slope of the hypocone, in the area enclosed between the praehypocrista and the ectohypocrista. It occludes with the disto-lingual slope of the lower M1. In the upper M1 of Le Moustier 1, the presence of an additional fissure determines the division of facet 12 in two parts (12a and 12b). The division of facet 12 occurs also in the lower M1. Finally, facet 13 develops along the disto-buccal slope of the protocone, distally to the crista obliqua. The opposing mandibular contact is found in the area enclosed between the praehypoconulidcristid and the posthypoconulidcristid.

The Neanderthal lower molars differ from those of *Homo sapiens*, by the presence of a large anterior fovea, usually distally bordered by a well developed mid-trigonid crest, which continuously connects the protoconid with the metaconid (Bailey, 2002a, 2002b, 2006). The mesial slope of the mid-trigonid crest is formed by facet 7 and facet 10, usually tending to coalesce, while the distal slope is constituted of facet 5 and 11.

In addition, on the upper first molar of Le Moustier 1, two flat worn enamelled areas, enclosing two dentinal islands, are identifiable on the tip of the protocone and hypocone. These additional facets are probably created during puncture-crushing (Gordon, 1984; Janis, 1990), and therefore have been labelled as tip crushing areas (pro and hyp).

5.3 Dental Chipping in the modern hunter-gatherers sample

The buccal side of the upper dentition of the modern hunter-gatherers included in the sample is frequently characterized (27%) by fractures, splintering and crushing. The dental chipping is localized in proximity of the metacone and paracone cusps, developing and inclining buccally (Fig. 5.2).

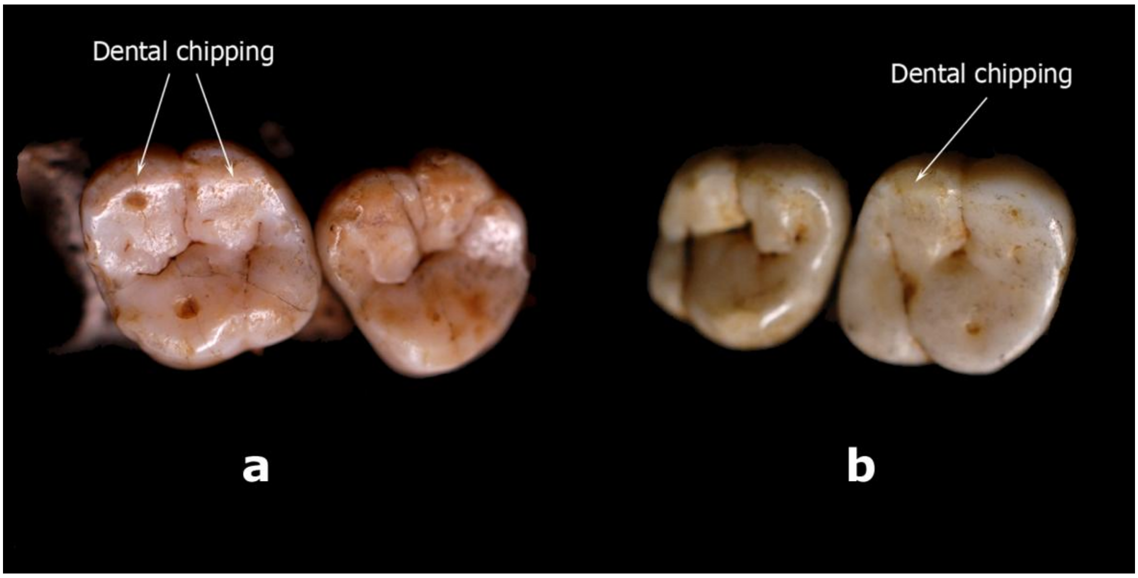


Figure 5.2 - Maxillary molars of modern hunter-gatherers showing dental chipping.

It is more developed in the meat-eaters group, especially in the Inuit, whereas is completely absent in the Bushmen. It occurs only in one Australian aborigine specimen. This chipping has been described by Turner II and Cadien (1969) and was termed as “pressure-chipping” among the Aleuts, the Eskimo and the northern Indians, suggesting the crushing of hard substances as bones, as one of the possible causes.

If the chipped areas are analyzed more in detail, it is possible to note flat and polished areas very similar to the occlusal wear facets. However, these areas in the upper molars do not have corresponding facets in the lower dentition, and therefore they cannot be produced during a normal chewing cycle. It is more likely to hypothesize that these types of facets are due to para-masticatory activities, such as holding objects during tool construction, etc. The analysis of the 3D occlusal compass shows clear differences in dip directions between the normal buccal facets (1, 2, 3 and 4) and the “chipping facets” (Fig. 5.3). Facet 1 and 4 are created by lateroretrusive movements, while facet 2 and 3 occlude during lateroprotrusive movements. The “chipping” facets instead point lingually, showing mediotrusive and medioprotrusive directions.

For this reason it is not possible to consider the “chipping” facets belonging to the chewing cycle, and hence they are not included into the quantitative analysis.

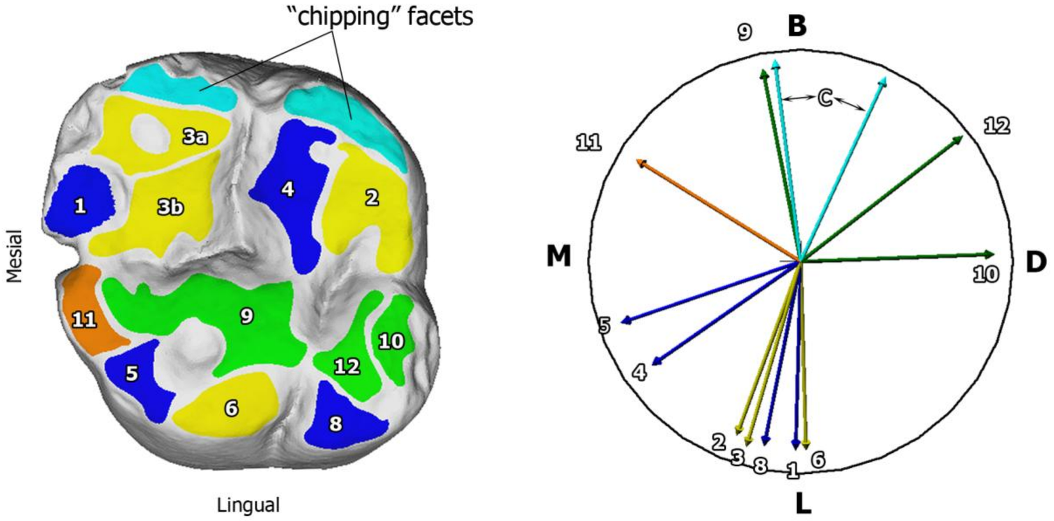


Figure 5.3 - Digital polygonal model of a maxillary molar showing the chipping facets. On the right, the corresponding 3D occlusal compass where the vectors (dip direction) of the chipping facets are highlighted. Occlusal movements: lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green) medioprotrusion (orange). Chipping facet directions in pale blue. Orientation: buccal (B); distal (D); lingual (L); mesial (M).

5.4 Occlusal Wear Pattern: General Overview

In general, in the complete study sample, buccal phase I facets (1, 2, 3 and 4) are most present in the occlusal wear pattern with a frequency higher than 90%, with the exception of facet 1.1 and 2.1, which occur with a lower percentage (45% and 19% respectively). Facet 3 and 4 occur in all the specimens included in the sample (Fig. 5.4).

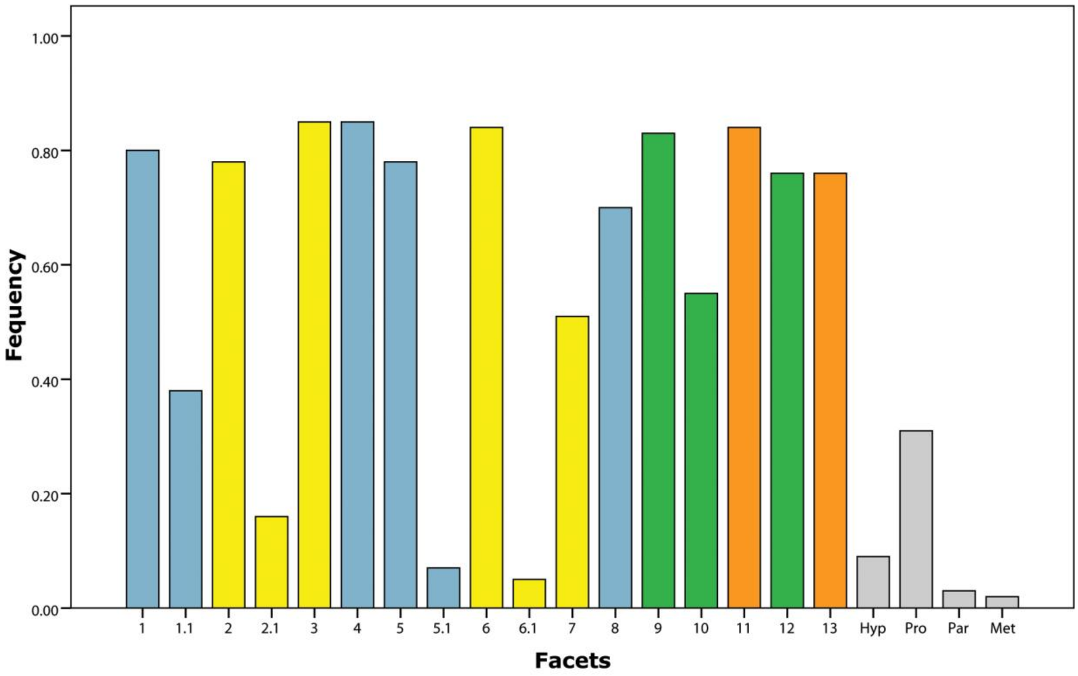


Figure 5.4 - Histogram showing the facet frequencies within the entire sample. Each wear facet is color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas in grey.

The frequency of the lingual phase I facets show lower percentages than those of the buccal facets. The protocone lingual facets (facet 5 and 6) are also quite common (92% and 99% respectively), whereas the facet 7 and 8 occur less frequently (60% and 82% respectively). This difference in frequency is affected by the reduction (or by the absence) of the hypocone cusp, characterizing the modern *Homo sapiens* sample. The phase II facets display a frequency slightly less pronounced than buccal phase I facets, which is particularly evident in facet 10 (64%). The tip crush areas are the less developed and they occur in less than 10% of the sample, with the exception of the protocone tip crush, displaying a frequency of about 37%.

5.4.1 Relative area

The buccal phase I facets are the most developed contact areas, and facet 3 is the largest wear facet (Fig. 5.5). The lingual phase I facets are less pronounced, showing larger occlusal contacts along the slopes of the protocone and smaller facets on the hypocone. The phase II facets display similar and relative large areas, where facet 9 represents one of the most developed wear facets. The tip crush areas are less pronounced, especially on the buccal cusps. Since the crushing areas are relatively small and less frequent, they will be no further considered in the quantitative analysis, with the exception of the relationship between relative area and cusp morphology.

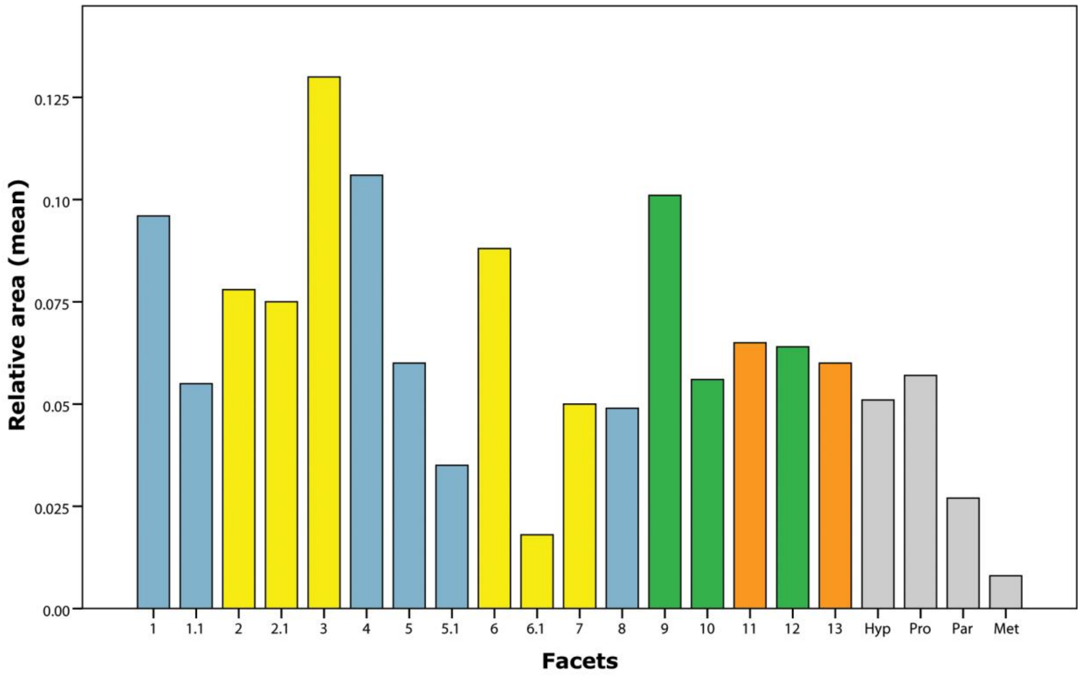


Figure 5.5 - Histogram illustrating the relative area of each wear facet within the entire sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas in grey.

As in the fossil group the number of specimens is relatively low, first and second upper molars with a slightly different degree of wear (2 and 3) have been included in the analysis in order to enlarge the sample size. This may increase the variability, due to differences in morphology between first and second molars and wear stages. If upper molars with different degree of wear are compared within the three main groups (Neanderthal, early *Homo sapiens* and modern hunter-gatherers), considering the relative buccal, lingual phase I and phase II areas, the one-way NPMANOVA analysis based on the pairwise comparison shows no statistically

significant differences (see Appendix D, Tab. D1). Comparing the relative areas between first and second upper molars within the Neanderthal (NEA) sample, the one-way NPMANOVA analysis does not display any statistically significant difference (see Appendix D, Tab. D2). Since the sample size of early *Homo sapiens* (EHS) maxillary molars consisted of only two specimens, the comparison between M^1 and M^2 in the EHS group was not carried out.
Within the modern hunter-gatherers sample (MHG), however, the relative wear facet areas of first molars result to be different from those of second molars (see Appendix D, Tab. D1). If we consider only the comparison between M^1 and M^2 within the Inuit and the Vancouver Islanders group (Fuegians, Australian aborigines and Bushmen are constituted by sample size of the M^1 or M2 groups which is lower than 3 specimens, therefore were not used in the statistical comparison), the results do not show a statistical significance level in the former group, while in the latter group the difference is significant (see Appendix D, Tab. D3).
This result may be affected by the non-homogenous hypocone absence, characterizing the Inuit and Vancouver Islanders sample (three and four specimens respectively), and always present in the Fuegians, Australian aborigines and Bushmen group. Despite that, the comparisons within the groups (with the exception of the Vancouver Islanders) do not show a high degree of difference, and consequently, the relative areas of first and second molars will be considered in the following statistical comparison.

5.4.2 Dip angle

The wear facets show a mean angle of approximately 20° (Fig. 5.6). The buccal phase I facets display an inclination higher than 20°, especially evident in facet 4 and 2.1 (27° in both facets). Facet 1.1 displays a rather flat area with a dip angle lower than 10°. The lingual phase I facets show higher dip angles, which become rather steep on the mesio-lingual slope of the protocone (facet 5) and on the slopes of the Carabelli cusp (facet 5.1 and 6.1). The phase II facets generally show flatter planes. The tip crush areas are characterized by low dip angles particularly marked on the lingual side, while on the buccal cusps, as on the metacone, the inclination show higher values.

Since the wear score system used in this study takes into account the cusp removal, the correlation between degrees of wear and dip angle probably occurs. If the dip angle of facets showing a wear stage 2 are compared with those possessing a wear stage 3 using the Mann-Whitney test, a *p* statistically significant is found in the mean angle and within the lingual, buccal phase I and phase II facets (see Appendix D, Tab. D4). Consequently, the following statistical comparative analysis of the dip angle will take into account only molars showing the same wear stage.

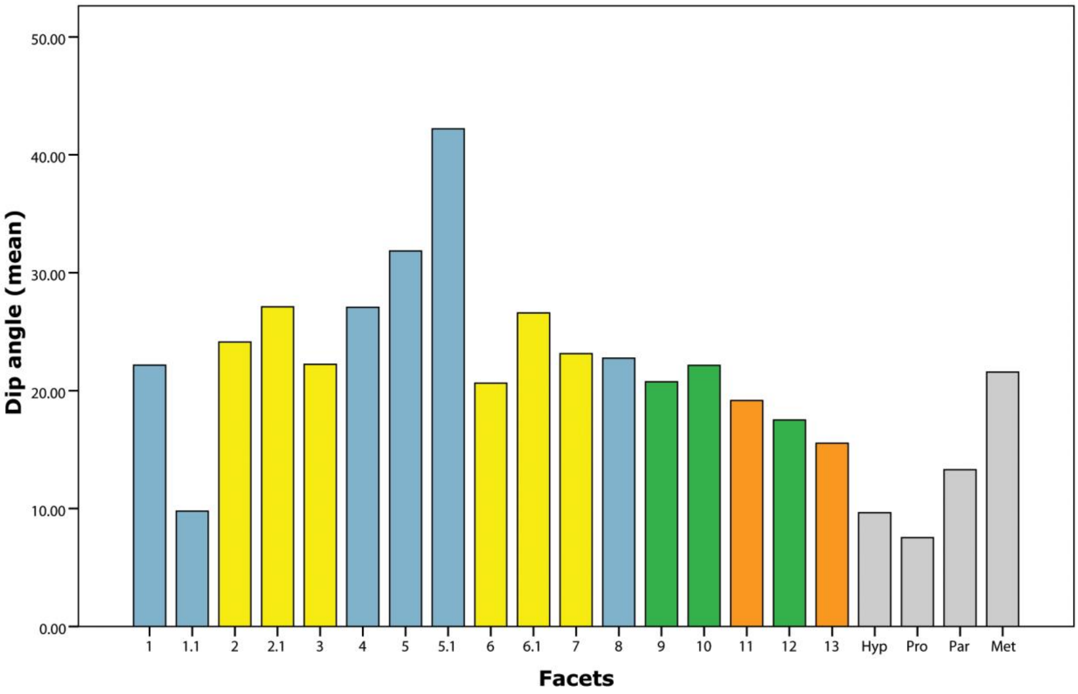


Figure 5.6 - Histogram displaying the mean dip angle of each wear facet within the entire sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas in grey.

5.4.3 3D Occlusal Relief Index

A high 3D occlusal relief index (or ORI) indicates an occlusal morphology rather complex, characterized by cups possessing steep slopes. If the ORI is plotted with the dip angle the linear correlation is not so evident, showing a low Coefficient of Determination relatively (R^2= 0.397) (Fig. 5.7). However if the ORI of upper molars with different degree of wear are compared between each other, molars with a wear stage 2 show higher ORI values than those with wear stage 3 (Fig. 5.8).

The following comparative analysis will consider only molars with similar stage of wear, although the Mann-Whitney test shows a *p* only close to the statistical significance level (see Appendix D, Tab. D5).

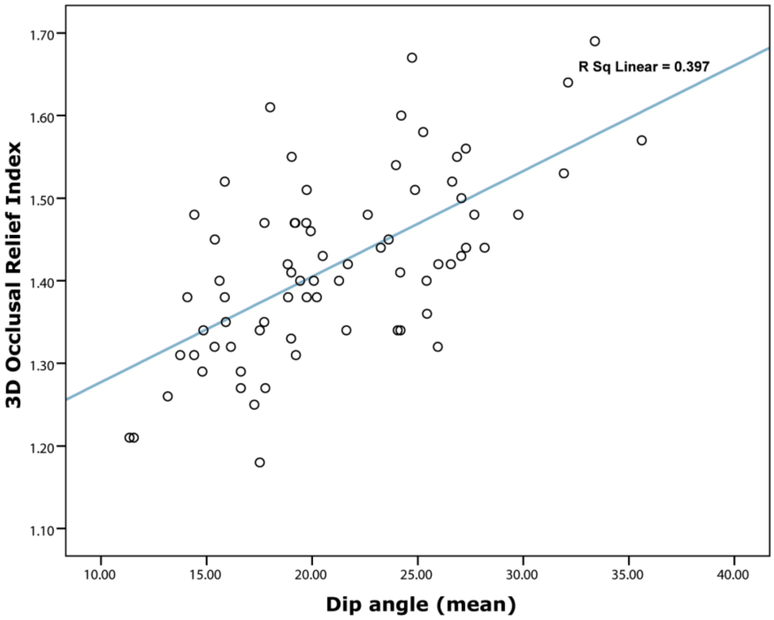


Figure 5.7 - Scatter plot showing the linear regression (based on the least squares method) between occlusal relief index (ORI), and dip angle (mean), and including the Coefficient of Determination (R sq. linear). The dip angle of each specimen was calculated considering the mean of all wear facet inclinations.

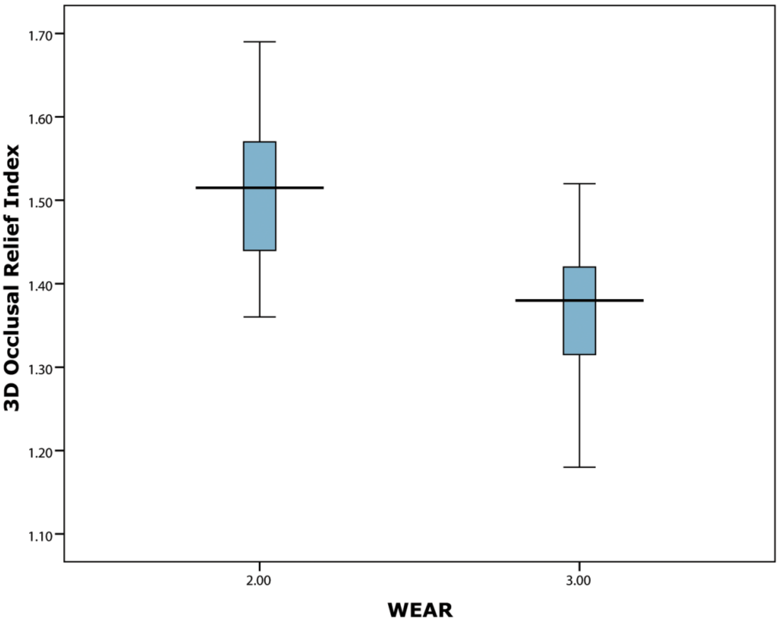


Figure 5.8 - Box plot illustrating the differences in occlusal relief index (ORI) related to the degree of wear (wear stage 2 and 3).

5.4.4 Dip direction

The phase I facets, both buccal and lingual, show two main and clearly distinctive dip directions, coinciding with lateroretrusive and lateroprotrusive movements (Fig. 5.9). However, the phase II facets, although clearly different from phase I facets, show an overlap of dip directions, in which case it is not possible to identify a full separation between mediotrusive and medioprotrusive movements.

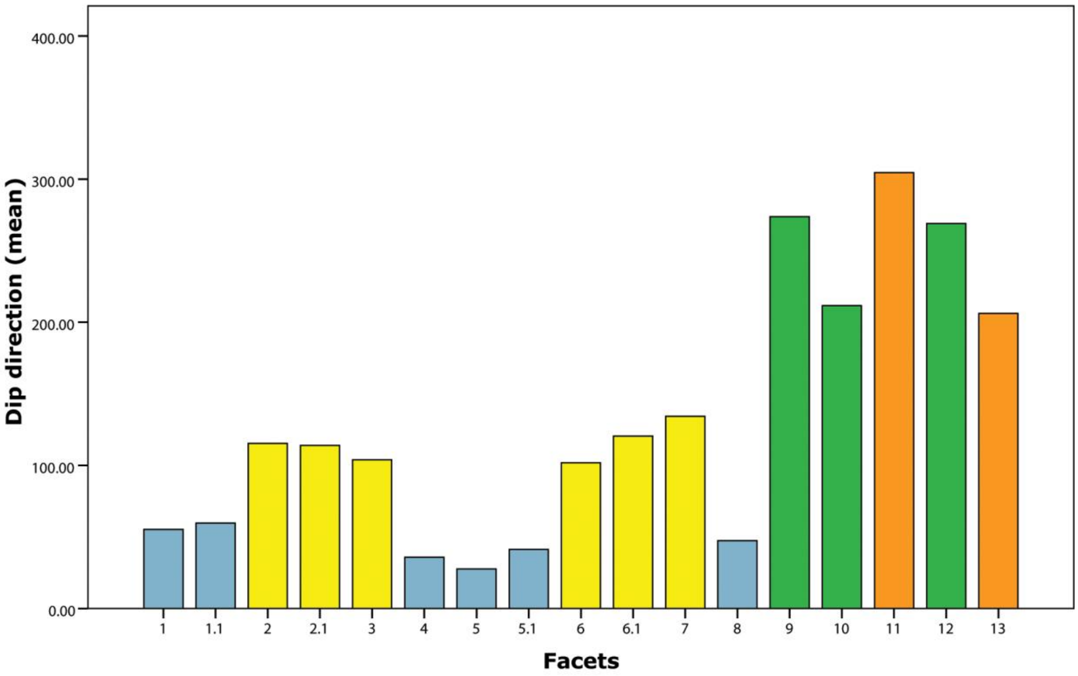


Figure 5.9 - Histogram displaying the dip direction (mean) within the entire sample. Each wear facet is color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange).

5.5 Modern hunter-gatherers

The modern hunter-gatherers (MHG) sample is characterized by almost total absence of the Carabelli wear facets (facet 5.1 and 6.1) and by a strong reduction in frequency of the lingual phase I facets developed along the hypocone slopes (facet 7 and 8) (Fig. 5.10). The buccal phase I facets (1, 2, 3 and 4) and facet 6 show the highest frequency (more than 90%). Facet 1.1 occurs in more than 50 % of the sample teeth, while facet 2.1 shows a low frequency (lower than 20%). The phase II wear facets are dominated by the presence of facet 9 and 11 (98% in both cases), while facet 10 shows a frequency lower than 50%. The tip crush areas are weekly pronounced, with the exception of the protocone tip crush which displays a frequency of about 30%.

5.5.1 Relative area

The buccal phase I facets are well developed, including the less frequent facet 1.1 and 2.1 (Fig. 5.11). Facet 3 is the largest occlusal wear area. The lingual wear facets are less pronounced and the only relatively large area is facet 6. Phase II facets are slightly more developed than lingual wear facets, and facet 9 shows one of the largest surfaces.

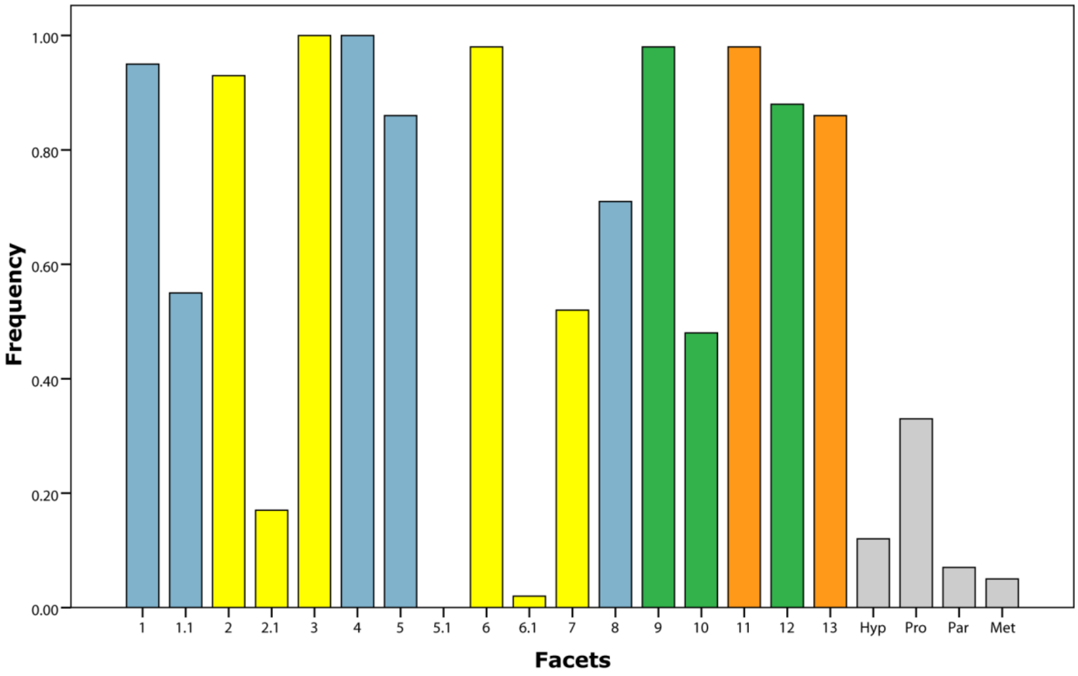


Figure 5.10 - Histogram showing the facet frequencies within the modern hunter-gatherers sample. Each wear facet is color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas in grey.

The tip crush areas, despite their low frequency, show relatively large occlusal surfaces which are particularly evident on the lingual cusps.

The buccal phase I facets are more developed in the Inuit, Vancouver Islanders and Fuegians groups, and less pronounced in the Bushmen and the Australian aboriginal sample (see Appendix D, Tab. D6). The statistical comparison, based on the Permutation *t* test, between the buccal phase I facets of the different MHG groups, does not show significant difference (see Appendix D, Tab. D7). On the other hand the Inuit, Vancouver Islanders and Fuegians are characterized by weakly developed lingual phase I facets which are prominent in the Bushmen and Australian aborigines group. The comparison between the MHG groups, based on the Permutation *t* test, shows a statistical significant difference between Bushmen and Inuit as well and between Bushmen and Fuegians (see Appendix D, Tab. D7). The phase II facets are equally distributed in all the MHG groups, with the exception of the Bushmen where these facets are less developed. The Permutation *t* test indicates a statistical difference between Bushmen and Inuit (see Appendix D, Tab. D7).

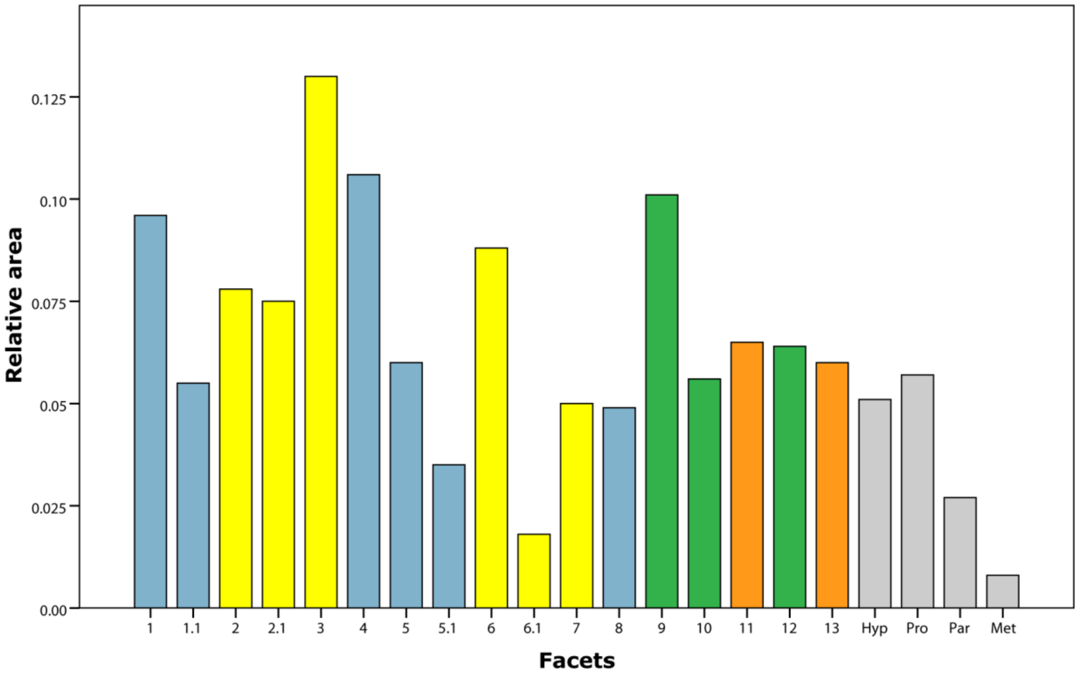


Figure 5.11 - Histogram presenting the relative area (mean) of each wear facet within the modern hunter-gatherers sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas in grey.

If the MHG are grouped in two separate samples, meat-eaters hunter-gatherers (Inuit, Vancouver Islanders and Fuegians) on one side and mixed-diet hunter-gatherers (Australian aborigines and Bushmen) on the other side (see Appendix D, Tab. D8), the statistical comparison based on the non-parametric Mann-Whitney test, shows differences more pronounced between the two groups (see Appendix D, Tab. D9). The comparison of the buccal phase I facets is close to the significance level, while in both lingual phase I facets and phase II facets, the differences result to be statistically significant between the meat-eaters and the mixed-diet hunter-gatherers.

If all the three variables are considered, they can be graphically represented by means of the ternary plot (Fig. 5.12). The MHG group shows a linear correlation between lingual and phase II facets. As the phase II facets increase, the relative areas of the lingual facets decrease. The Inuit, Vancouver Islanders and Fuegians display a pronounced overlap, forming one main group. The Bushmen seem to be separated, while the Australian aborigines plot between meat-eaters and Bushmen, although they are closer to the African group.

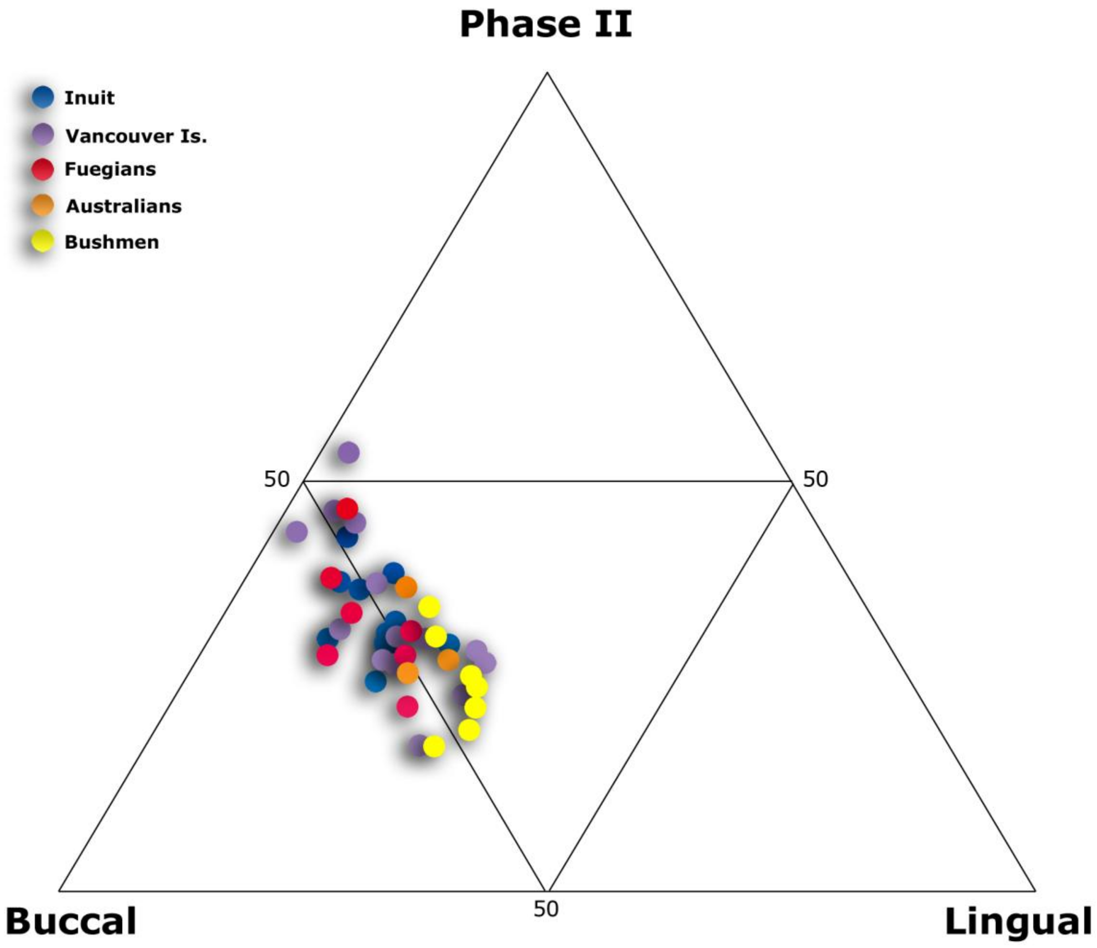


Figure 5.12 - Ternary plot illustrating the distribution of the different groups (Inuit, Vancouver Islanders, Fuegians, Australian aborigines and Bushmen) within the modern hunter-gatherers sample based on the proportions of the buccal, lingual and phase II facet areas.

A one-way NPMANOVA analysis is applied to the MHG sample based on the pairwise comparison, including values corrected with Bonferroni *post-hoc* analysis (see Appendix D, Tab.

D10). The non-corrected *p* values show statistically significant differences between the meat-eaters group (Inuit, Vancouver Islanders and Fuegians) and Bushmen. The Australian aborigines result to be similar to both meat-eaters and Bushmen. If the Bonferroni correction is taken into account, statistically significant differences are found only between Bushmen and Inuit, while the comparison between Bushmen and Fuegians is close to the significance level. In addition, a Canonical Variates Analysis (CVA) has been used to create a scatter plot of specimens along the two first canonical axes, producing maximal and second to maximal separation between all groups (multigroup discriminant analysis) (Hammer & Harper, 2006) (Fig. 5.13). The CVA plot shows similar results than those obtained using the ternary plot. The meat-eaters groups show a high degree of overlap, plotting toward the negative values of the axis 1. The Bushmen sample, instead, plots towards positive values of the axis 1 and 2. The specimen S16 results to be an outlier, plotting towards negative values of the axis 2. The Australian aborigines overlap with the meat-eaters group, but they plot closer to the Bushmen group.

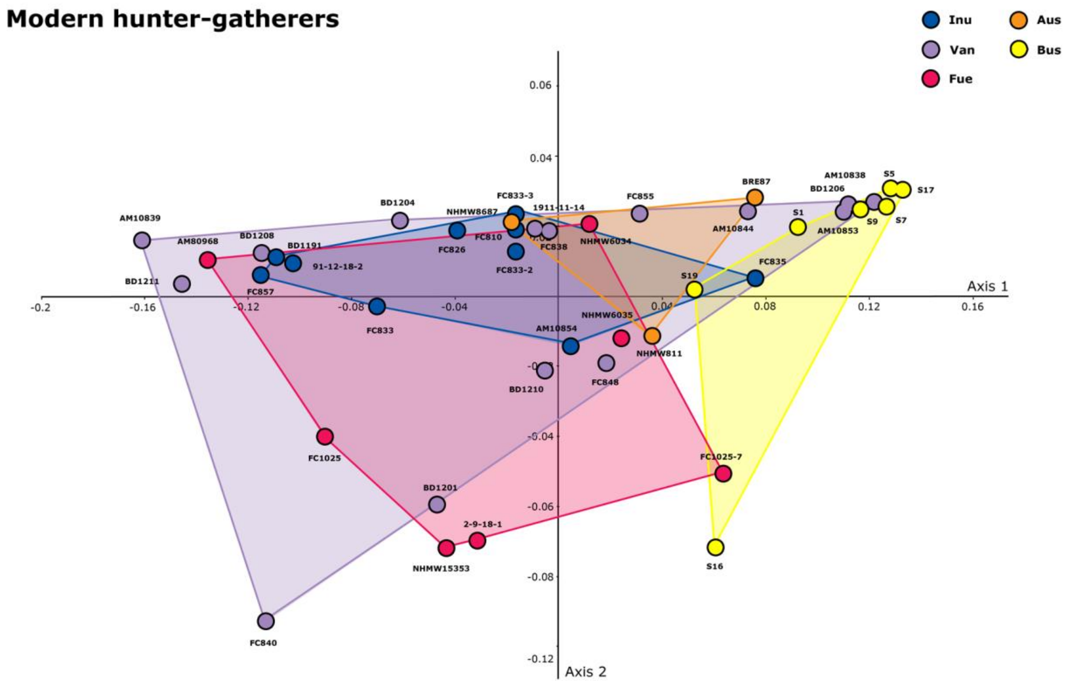


Figure 5.13 - CVA scatter plot based on the analysis of the relative areas of the buccal, lingual and phase II facets, showing the distribution of the modern hunter-gatherer groups. Inuit (Inu); Vancouver Islanders (Van); Fuegians (Fue); Australian aborigines (Aus); Bushmen (Bus).

5.5.2 Dip angle

The facets show overall a dip angle of about 20° (Fig. 5.14). The buccal phase I facets possess a slightly steeper inclination, which is particularly marked in facet 4. Within the lingual facets, facet 5 represents the steepest occlusal contact, while the other facets show similar values. The phase II facets are flatter, showing dip angles lower than 20°. The tip crushing areas display a high variability characterized by the protocone and hypocone tip crush which constitute the flattest facets of the entire occlusal surface and by the metacone and paracone tip crush showing a higher inclination, especially pronounced on the metacone cusp.

Upper molars displaying wear stage 2 in the MHG sample occur only in a single specimen in the Inuit, Fuegians and Bushmen groups. They are lacking in the Australian aboriginal group. Therefore the subsequent comparative analysis within the MHG sample will take into account only upper molars showing wear stage 3.

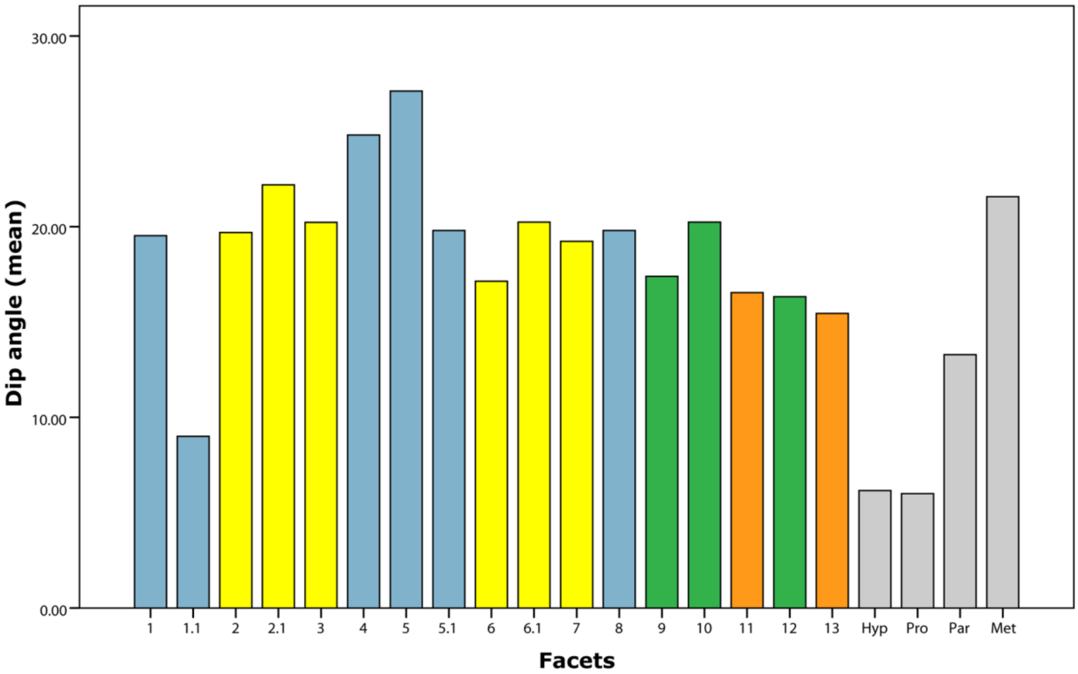


Figure 5.14 - Histogram displaying the mean dip angle of each wear facet within the modern hunter-gatherers sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas in grey.

The buccal phase I facets are relatively steep in the Bushmen group, while in the Inuit, Vancouver Islanders and Fuegians show a lower and uniform degree of inclination. The Australian aborigines possess the flattest buccal wear facets (see Appendix D, Tab. D11).

However the Permutation *t* test does not show any statistically significant difference between the MHG groups (see Appendix D, Tab. D12).

If the inclination of the lingual facets is considered, all the MHG groups show similar values with the exception of the Australian aborigines displaying very flat occlusal areas and the Vancouver Islanders which are characterized by a slightly lower dip angles (see Appendix D, Tab. D11).

Also in this case, the statistical comparison between the different MHG groups does not show any significant difference (see Appendix D, Tab. D12). The phase II facets are overall less steep and the difference is less pronounced. In fact, the results from the Permutation *t* test do not show any statistical significance (see Appendix D, Tab. D12). If for each specimen a mean dip angle is calculated, the descriptive analysis shows that the Australian aborigines are characterized by very low facet inclination (see Appendix D, Tab. D11). However, the statistical comparison does not differentiate the Australian aborigines from the other MHG groups (see Appendix D, Tab. D12). The use of the Mann-Whitney pairwise comparison between meat-eaters and mixed diet group does not reveal any statistically significant difference within the buccal, lingual phase I, phase II and the overall occlusal area (see Appendix D, Tab. D13 and D14).

5.5.3 Occlusal Relief Index

The Inuit group displays the highest ORI, while the Australian aborigines are characterized by the lowest ORI values. Vancouver Islanders, Fuegians and Bushmen show similar results, comprised between the Inuit and Australian aboriginal group (see Appendix D, Tab. D15). However, the statistical comparison (Permutation *t* test) does not highlight any significant differences (see Appendix D, Tab. D16).

If the MHG samples are grouped into meat-eaters and mixed-diet hunter-gatherers (see Appendix D, Tab. D17), the comparison (Mann-Whitney's test) does not show any statistically significant difference (see Appendix D, Tab. D18).

5.5.4 Dip direction

The lateroretrusive (LRT) and lateroprotrusive (LPT) movements show a clear difference between each other. The phase II facets confirm the great overlap seen in entire sample, where facet 11 is directed in the mediotrusive (MT) + immediate side shift (ISS) compass area, and facet 10 in the medioprotrusive (MPT) one (Fig. 5.15).

Australians aborigines are characterized by a high variability in the jaw movements which is also confirmed by the Rayleigh's test, where the *p* values are higher than the significance level, indicating that the data is distributed uniformly, showing no evidence for a preferred direction. In the Inuit group the LRT movements are more restricted and tend to overlap with LPT movements which show a high variability. The Bushmen display a low variability in both LRT and LPT movements (see Appendix D, Tab. D19).

The pairwise comparison based on the Watson-Williams test is applied in order to determine if the mean angles between two or more samples differ significantly (see Appendix D, Tab. D20). The LRT analysis shows a statistically significant difference only between Bushmen and Inuit. In the LPT comparison, the Inuit result to be statistically different from the Australian aborigines and Bushmen, while difference is found also between Fuegians and Bushmen. The analysis of the phase II facets dip directions, MT and MPT, shows no statistically significant difference between the groups.

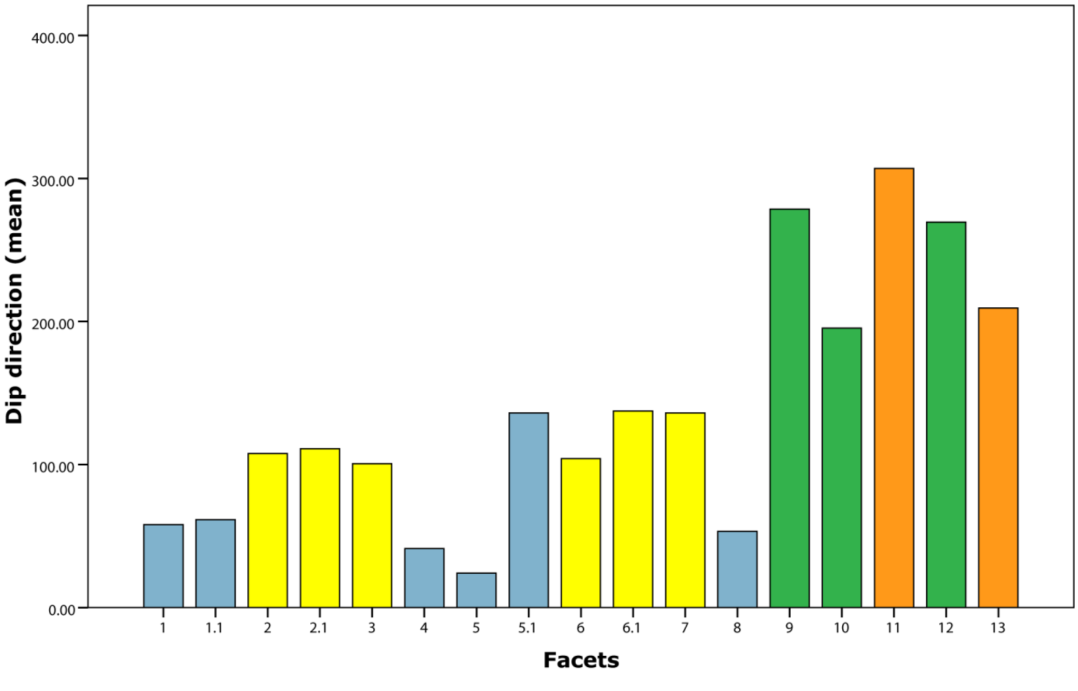


Figure 5.15 - Histogram illustrating the dip direction (mean) of each wear facet within the modern hunter-gatherers sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange).

If the MHG sample is separated in meat-eaters and mixed-diet groups a general increase of variability in the LRT movements of the mixed-diet groups is notable, while the meat-eaters sample shows a higher variability in the LPT, MT and MPT wear facets (see Appendix D, Tab. D21). The Watson-Williams test shows a statistically significant difference in the LRT and LPT movements between the two groups, while the comparative results of the MT and MPT facets are not significant (see Appendix D, Tab. D22).

5.6 Neanderthals

The Neanderthal group (NEA) is characterized by a high facet frequency (Fig. 5.16). The facet 3, 4, 5, 6, 8, 9 and 11 occur in all NEA specimens. The buccal phase I facets 1 and 2 are slightly less frequent (95% and 84% respectively), whereas facet 1.1 and 2.1 show low percentages values (37% and 16% respectively). The Carabelli facets are more frequent than those of MHG (21% facet 5.1), and facet 7 reaches a frequency close to 60%. The phase II facets are all rather common occurring with a frequency higher than 90% (facet 10 and 12 reach a frequency of 89%). The tip crushing areas are absent on the buccal cusps (metacone and paracone), while they occur frequently only on the protocone (protocone, 42%; hypocone, 5%).

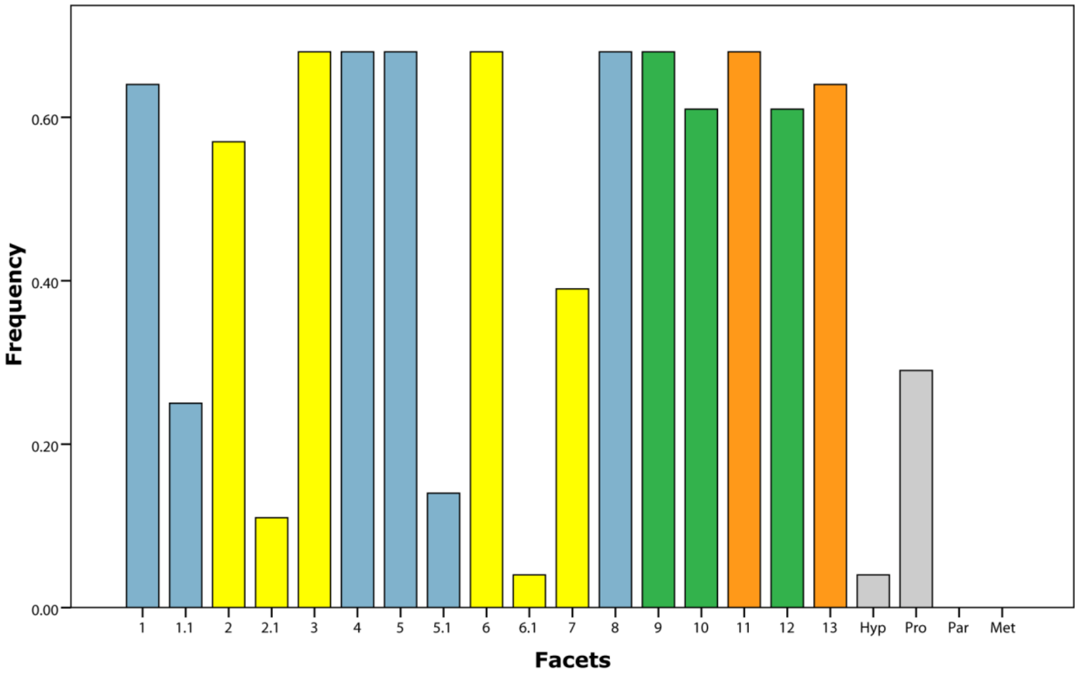


Figure 5.16 - Histogram showing the facet frequencies within the Neanderthal sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas are in grey.

5.6.1 Geographical grouping

In order to evaluate if the occlusal wear pattern differs in relation to different geographical and climate areas, the NEA sample has been divided in three smaller groups, which represent three different and specific environments:

1. Deciduous woodland
2. Mediterranean evergreen
3. Steppe/Coniferous forest

The deciduous woodland sample is constituted only by the Krapina specimens who occupied the northern Croatia during the Oxygen Isotope Stage (OIS) 5e, which was a relatively warm period, with vegetation mostly consisted of deciduous forest and Mediterranean woodland (Van Andel & Tzedakis, 1996). The Mediterranean evergreen group is composed of Amud 1, Tabun 1 and Shanidar 2. Amud 1 and Tabun 1 lived in the same territory (Israel) at different times (OIS 3 and OIS 5e respectively). During OIS 5 the climate conditions of the Levantine territory were similar to the present day, with warm temperature and vegetation constituted by a Mediterranean evergreen. During OIS 3 the climate was characterized by wetter and colder conditions than those present during OIS 5, which probably caused an increase in the forest coverage (Hallin, 2002, 2008). Although the Levantine area during these two periods was characterized by a slightly different climate conditions, it is reasonable to hypothesize a similar warm environment, characterized by an open vegetation consisted of shrubs and grassland evergreen. Consequently, the two NEA specimens are included in the same group. The information regarding the dating of Shanidar sample is dubious and incomplete, enclosed in a period of time comprised between OIS 6 and OIS 4 (Cowgill et al., 2007). It is therefore difficult to place Shanidar 2 in an accurate environmental context. However, the faunal assemblage indicates an open environment constituted by shrub vegetation which probably shows some similarity to Mediterranean zone, and therefore Shanidar 2 will be considered as part of the Mediterranean group. The steppe/coniferous forest group is constituted by the specimens Monsempron 2 and 3, Le Moustier 1 and Vindija V259. Although the steppe and the coniferous forest represent two different types of vegetation, are both present in cold environments which may have provided similar food sources. Little information is available for the Monsempron sample. Although the beginning of the Würm I has been indicated as possible dating, corresponding to a warm climate (Oakley et al., 1971), the presence of the reindeer in the faunal assemblage and the analysis of the stone tool technology suggests a colder climate. It probably corresponds to the end of OIS 4 or the beginning of OIS 3 (Quintard et al., 2007), and consequently it is possible to hypothesize vegetation constituted by steppe and/or coniferous forest. Le Moustier occupied the southern western France around 41 BP (Mellars & Grün, 1991) which corresponds to a colder climate, also confirmed by the presence of the reindeer in the faunal assemblage. The specimen Vindija V259 lived in the same period like Le Moustier (Krings et al., 2000), occupying the northern Croatia, which was characterized by a colder climate and is consequently considered to belong to the steppe/coniferous forest group.

5.6.2 Relative area

The buccal phase I facets are less prominent, with the exception of facet 3 and 4 which represent large occlusal contact areas (Fig. 5.17). Facet 2 results to be less developed with a relative area slightly larger than facet 2.1. The lingual phase I facets are quite pronounced along the slopes of the protocone. In fact, facet 6 represents the largest occlusal wear facet in the entire NEA sample.

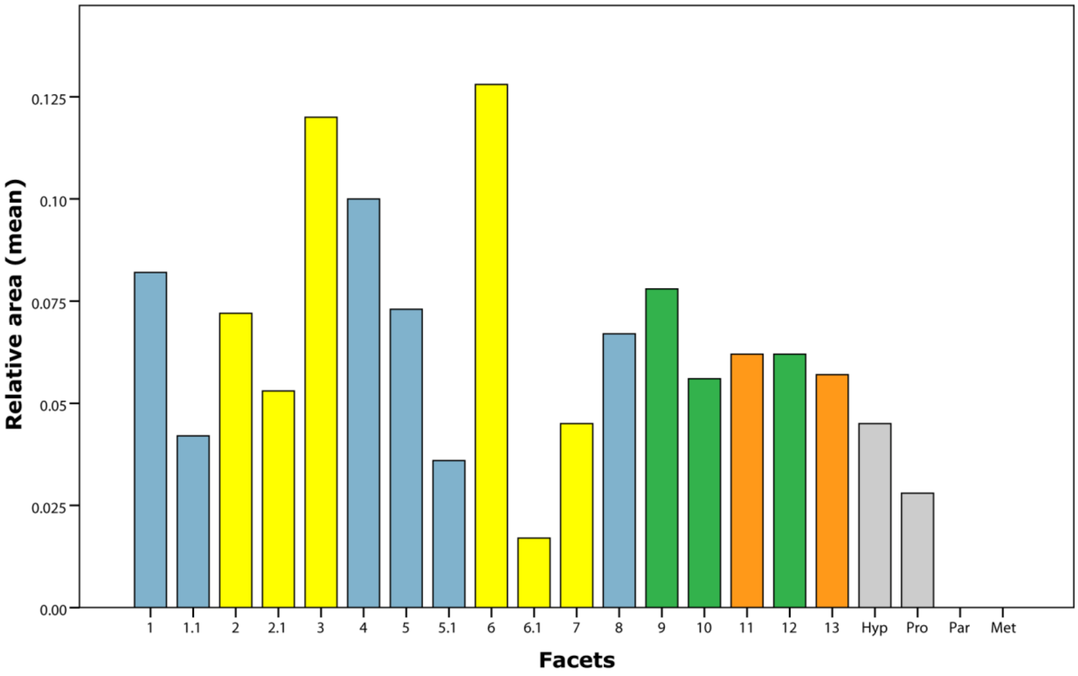


Figure 5.17 - Histogram displaying the relative area of each wear facet within the Neanderthal sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas are in grey.

The hypocone lingual facets are less developed, especially evident in facet 7. The Carabelli facets, although characterized by small wear facets, represent an important contact area during occlusion (facet 5.1 constitutes the 3.5% of the entire occlusal wear area). The phase II facets are overall less pronounced, with a relative size between 5 and 6% of the whole occlusal wear area, with the exception of facet 9 which constitutes a large contact area. Although the hypocone tip crush area results to be scarcely frequent, its relative size is larger than the protocone tip crush area (4.5% and 2.8% of the total amount of the occlusal wear respectively).

The deciduous forest group (DWN) is characterized by weakly developed buccal phase I facets (36.5%). Similar results are found in the Mediterranean group (MEN), while the steppe/coniferous forest (SCN) specimens show more developed buccal facets (44.5%) (see Appendix D, Tab. D23). Using the Permutation *t* test for the comparisons, the results obtained do not show any statistically significant difference, although the difference between the SCN group and DWN group is close to the significance level (see Appendix D, Tab. D24). The lingual phase I facets better distinguish the NEA groups. In fact, the DWN specimens show highly developed lingual facets which are reduced in the MEN group and strongly reduced in the SCN sample (see Appendix D, Tab. D23). The statistical comparison results to be statistically significant between the DWN and SCN groups, while the *p* value is close to the significance level in the comparison between the MEN and SCN specimens (see Appendix D, Tab. D24). The phase II facets show values more similar between the three groups, although in the SCN these facets are more developed and contrary less pronounced in the DWN sample (see Appendix D, Tab. D23). The comparative results do not show statistical significance (see Appendix D, Tab. D24).

The ternary plot derived from proportions of the three relative main areas (buccal, lingual and phase II facets), shows a separation of the DWN group which is characterized by a strong lingual development and less pronounced buccal and phase II facets Fig. 5.18). The SCN specimens display a considerable reduction of the lingual phase I facets and an increase of the buccal wear facets. The MEN sample plots centrally showing the three relative areas equally distributed, overlapping with the DWN group. The multivariate analysis (one-way NPMANOVA) shows a statistically significant difference only between DWN and SCN (see Appendix D, Tab. D25). The CVA scatter plot shows a clear separation between the DWN and SCN groups (Fig. 5.19).

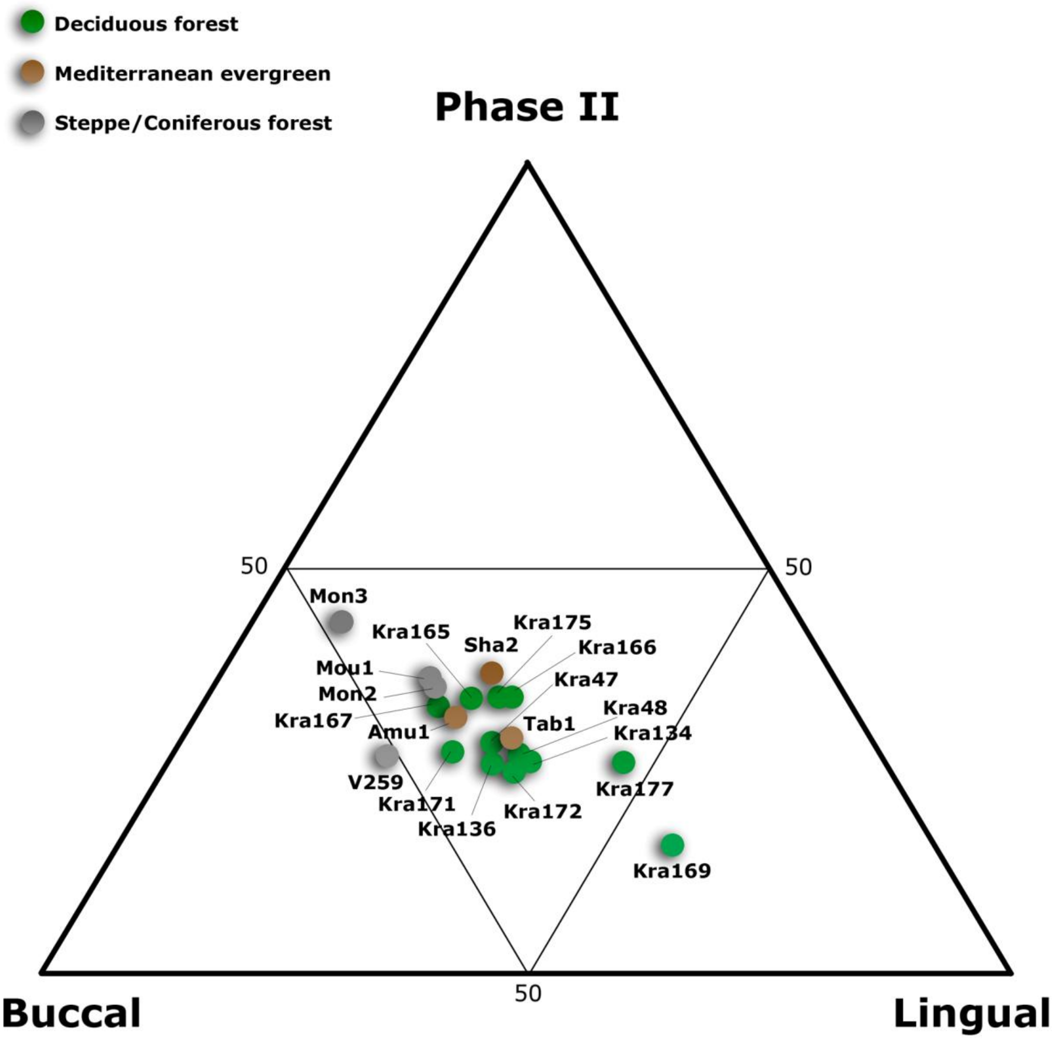


Figure 5.18 - Ternary plot illustrating the distribution of the Neanderthal groups considering the proportions of buccal, lingual and phase II facet areas. The Neanderthal sample is divided into three groups taking into account the ecogeographical variation (Deciduous woodland, Mediterranean evergreen and Steppe/Coniferous forest).

The DWN specimens are mainly distributed along the intersection of the two CVA axes, with two outliers (Krapina 177 and 169) on the Southeast quadrant, while the SCN group is distributed on the northwest quadrant. The MEN are distributed along the axes intersection, overlapping with the DWN, showing a separation from the SCN group.

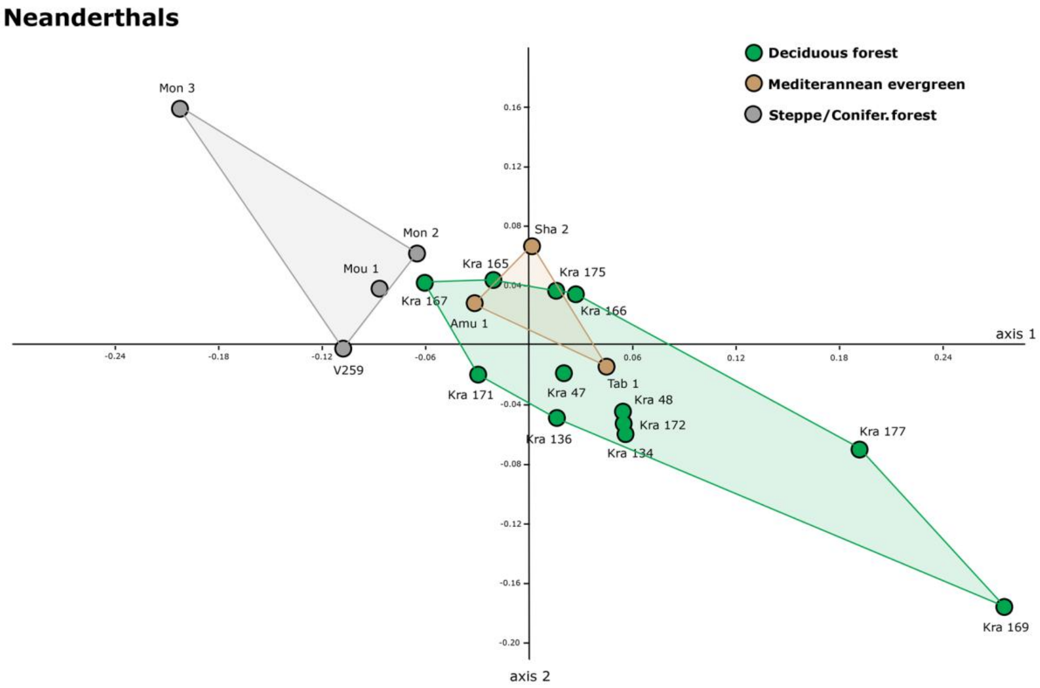


Figure 5.19 - CVA scatter plot based on the relative areas of buccal, lingual and phase II facets showing the distribution of Neanderthal ecogeographic groups (Deciduous woodland, Mediterranean evergreen and Steppe/Coniferous forest).

5.6.3 Dip angle

The occlusal wear facets show generally a high inclination between 20° and 30° (Fig. 5.20). The buccal phase I facets are rather steep, showing similar values of about 30° with the exception of facet 1.1 being relatively flat with a dip angle of about 11°. The lingual phase I facets display a slightly lower inclination than those of buccal facets with the exception of the occlusal contact developed mesio-lingually as facets 5, 5.1 and 6.1 (36°, 40° and 39° respectively) representing the wear facets with the steepest inclination in the NEA group. The phase II facets are characterized by a lower inclination, particularly evident in facet 12 and 13 (17° and 14° respectively).

Since dip angles change between the two different wear stages, the comparison within the NEA group is possible only taking into account specimens with the same degree of wear. A statistical comparative analysis cannot be carried out because the NEA groups based on the different type of vegetation are constituted by a small sample size (less than three specimens), with the only exception of the DWN for wear stage 2 (11 specimens) and the MEN group for wear stage 3 (3 specimens).

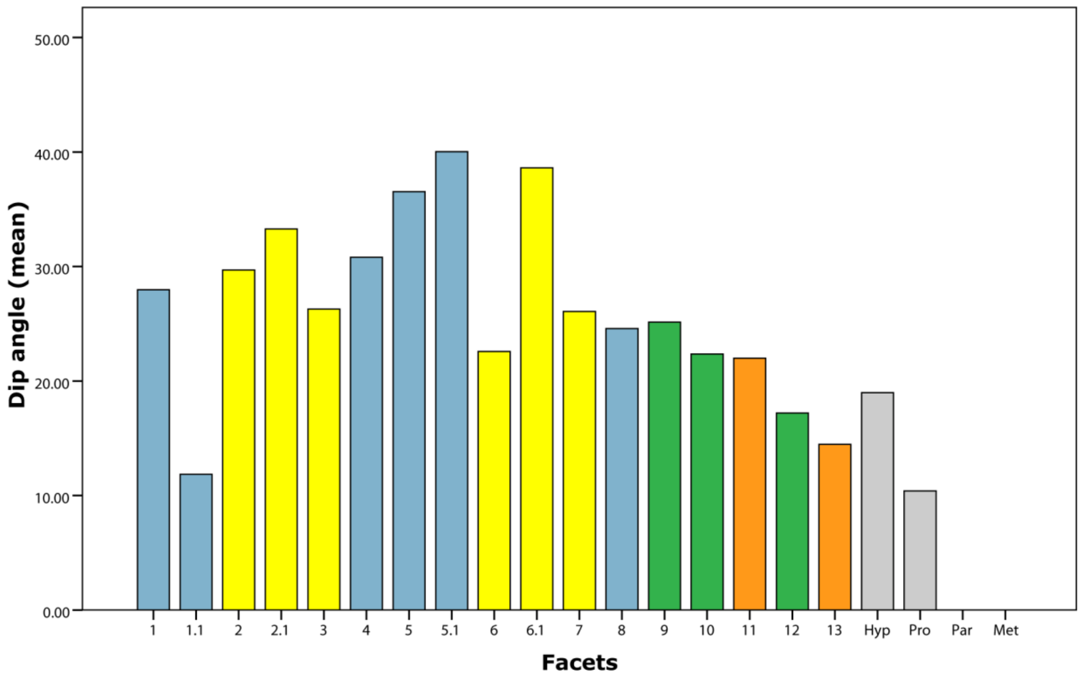


Figure 5.20 - Histogram presenting the mean dip angle of each facet within the Neanderthal sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas are in grey.

5.6.4 3D Occlusal Relief Index

For the same reason as it is shown above for the dip angle, the division of the NEA groups considering the wear stage 2 and 3 reduces excessively the sample size (less than three specimens) and therefore it is not possible to compute any statistical comparative analysis.

5.6.5 Dip direction

The LRT facets show a clear dip direction comprised between 20° and 50°, resulting to be distinctly separated from the LPT facets (100°-130°). The phase II facets show a strong overlap in dip directions caused by the facets 10 and 11 which point in the MPT and MT compass area respectively (Fig. 5.21).

Within the three vegetation groups, the DWN shows LRT values of about 32°, with a high variability, whereas the MEN and SCF groups are characterized by a LRT direction of about 45°. The LPT directions show similar values between the three groups. The phase II facets are characterized by a strong overlap, with a uniform direction, as indicated by the *p* values in the case of the MT facets of the MEN and the MPT facets of the DWN and MEN groups obtained using the Raylegh's test (see Appendix D, Tab. D26). The statistical comparison based on the Watson-Williams test shows strong similarity in dip directions between the three groups, finding a statistically significant difference only between the MT facets of DWN and MEN groups (see Appendix D, Tab. D27).

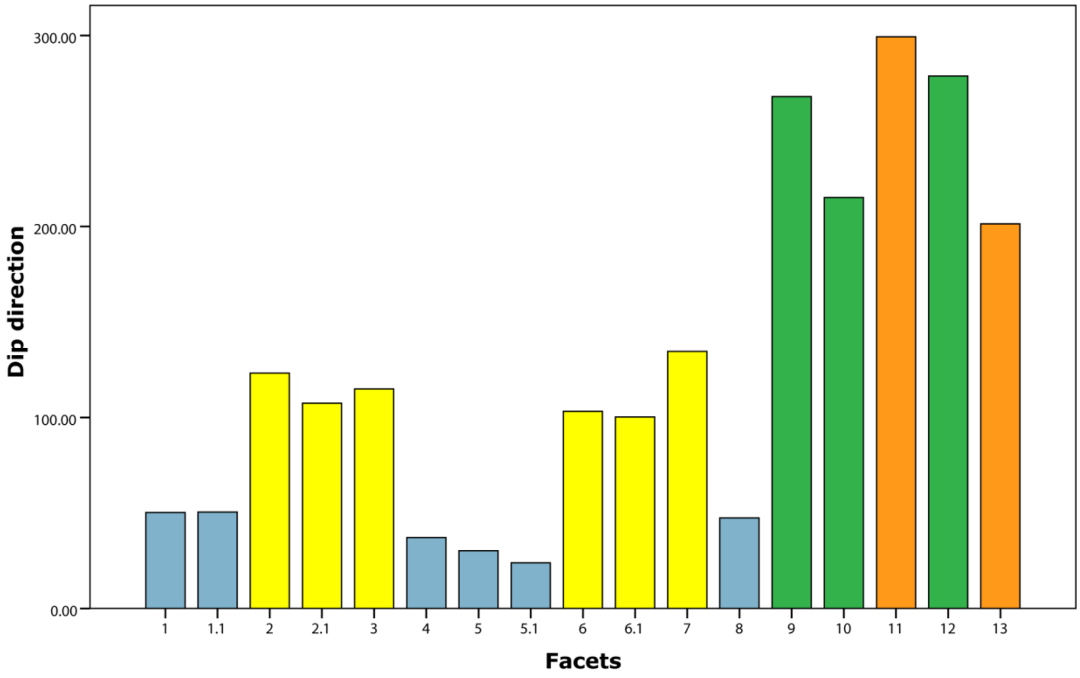


Figure 5.21 - Histogram illustrating the dip direction (mean) of each wear facet within the Neanderthal sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange).

5.7 Early *Homo sapiens*

In the earl *Homo sapiens* (EHS) sample most of the main facets are present, showing a frequency higher than 90% (Fig. 5.22). Considering the buccal phase I facets, the facets 2, 3 and 4 always occur, while facet 1 is slightly less frequent (92%), and facet 1.1 and 2.1 show a frequency of 25% and 33% respectively. The protocone lingual facets are present in 100% of the sample, whereas the hypocone wear facets display a lower frequency (92% in both cases). The Carabelli occlusal contacts reach a percentage of about 17%. The phase II facets are quite frequent (higher than 90%), wherein facet 11 is present in 100% of the sample, while facet 10 shows a lower frequency (83%). The tip crushing areas are completely absent on the buccal cusps, while on the lingual cusps they show a moderate frequency (40% on the protocone and 17% on the hypocone).

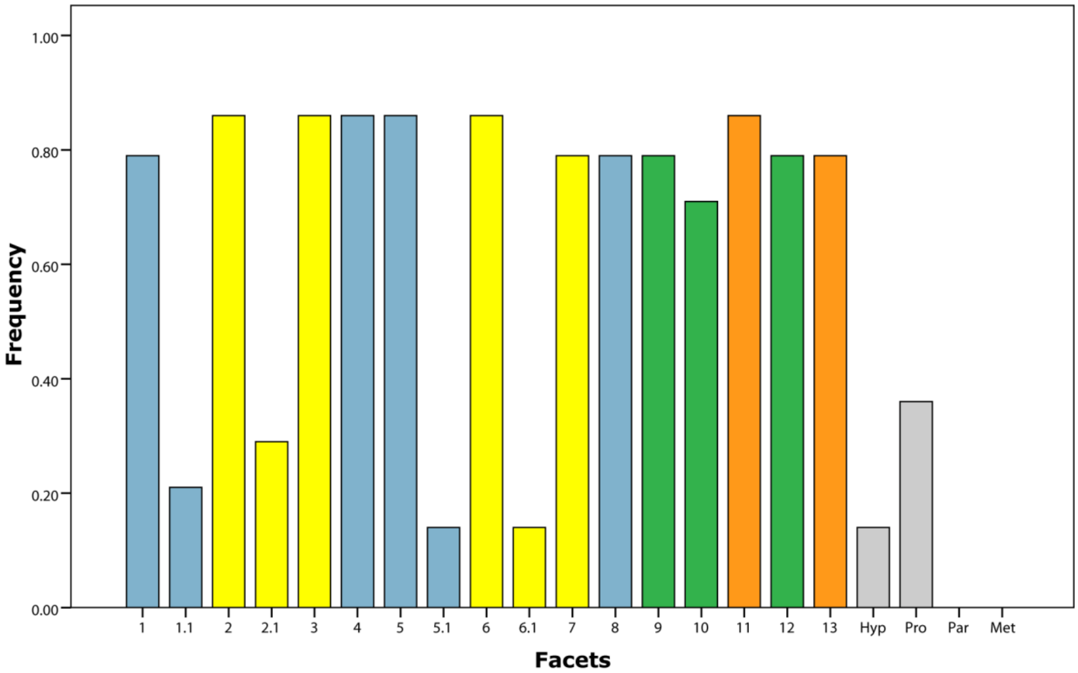


Figure 5.22 - Histogram displaying the facet frequencies within the early *Homo sapiens* sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas are in grey.

5.7.1 Geographical grouping

The EHS sample is constituted by the Qafzeh specimens (N=7) who occupied the Levantine territory during the Middle Paleolithic, in the OIS 5d and by five other specimens which lived in Europe at different places during the Upper Paleolithic, between OIS 3 and OIS 2. The Qafzeh environment was characterized by hot and dry climate conditions (Hallin et al., 2008) with a vegetation mainly constituted by a Mediterranean evergreen (Van Andel & Tzedakis, 1996). Mladeč lived in the central Moravia at the end of OIS 3, where the climate conditions were cold, as indicate by the faunal assemblage. However,no direct information regarding the vegetation is available, but it can be argued that the vegetation would have been similar to that from Dolni Věstonice because these two sites are geographically and temporary close (El Zaatari, 2007). The pollen analysis from the Dolni Věstonice indicates a vegetation mainly constituted by steppe and coniferous forest (Svobodová, 1991).

Barma Grande 3 and 4 occupied the Ligurian coastlines in northern Italy between the transition from OIS 3 and OIS 2 where the vegetation was mostly characterized by open environments and in less quantity by coniferous forest (Follieri et al. 1998; Watts et al. 1996). The Sungir specimen occupied the central Russia at the end of OIS 3, a temporal period characterized by a cold and continental climate, where the vegetation was constituted by steppe and coniferous forest (Buzhilova, 2005). Pataud 224 was found in southwestern France and dated 22 BP which corresponds to the OIS 2. The climate was dry and cold and the vegetation composed of coniferous forest (Théry-Parisot, 2002).

Therefore, based on the environmental information available, it is reasonable to divide the EHS sample in two main groups:

1. Mediterranean evergreen
2. Steppe/Coniferous forest

The Mediterranean group (MEHS) is entirely consisted of the Qafzeh specimens, while the Steppe/Coniferous forest group (SEHS) encompasses all the other EHS specimens (Mladeč, Barma Grande 3 and 4, Sungir 2, Pataud 224).

5.7.2 Relative area

In the EHS group facet 9 results to be the largest wear area of the entire occlusal surface (Fig. 5.23). The buccal phase I facets are slightly more developed than those of NEA, as evident in facet 1. Moreover it is interesting to note that facet 2.1 is larger than facet 2, and also facet 1.1 shows a relatively large occlusal area.

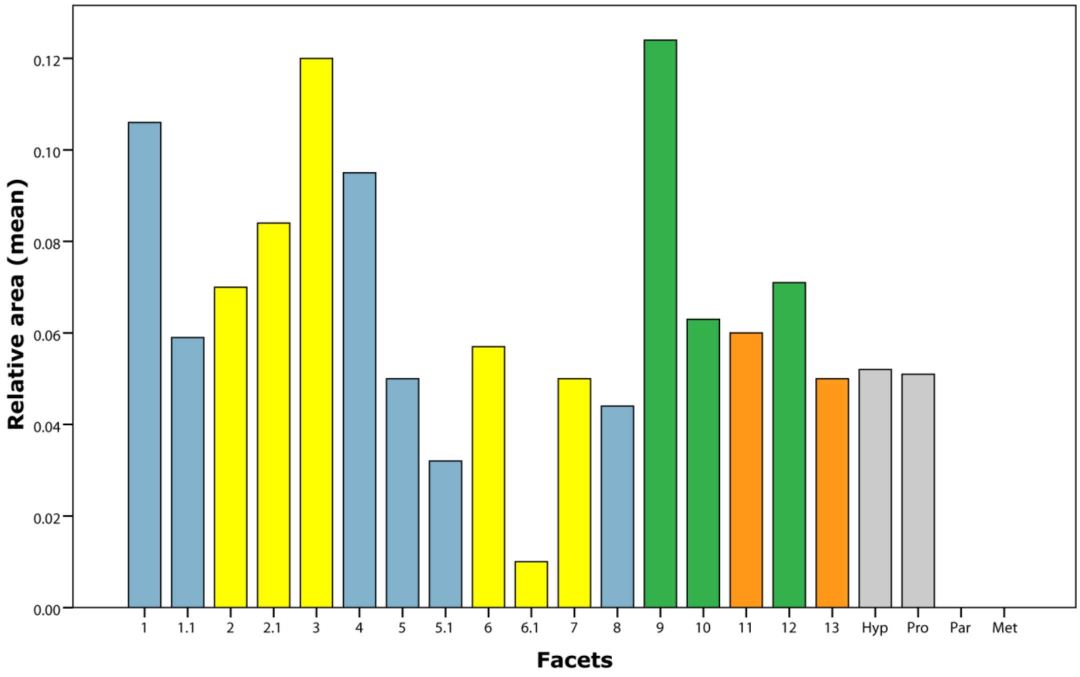


Figure 5.23 - Histogram showing the relative area of each facet within the early *Homo sapiens* sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas are in grey.

The lingual phase I facets are scarcely pronounced on both protocone and hypocone. The Carabelli facets constitute about 3% and 1% (facet 5.1 and 6.1 respectively) of the total occlusal wear area. The phase II facets are well developed, as well as the protocone and hypocone tip crush areas.

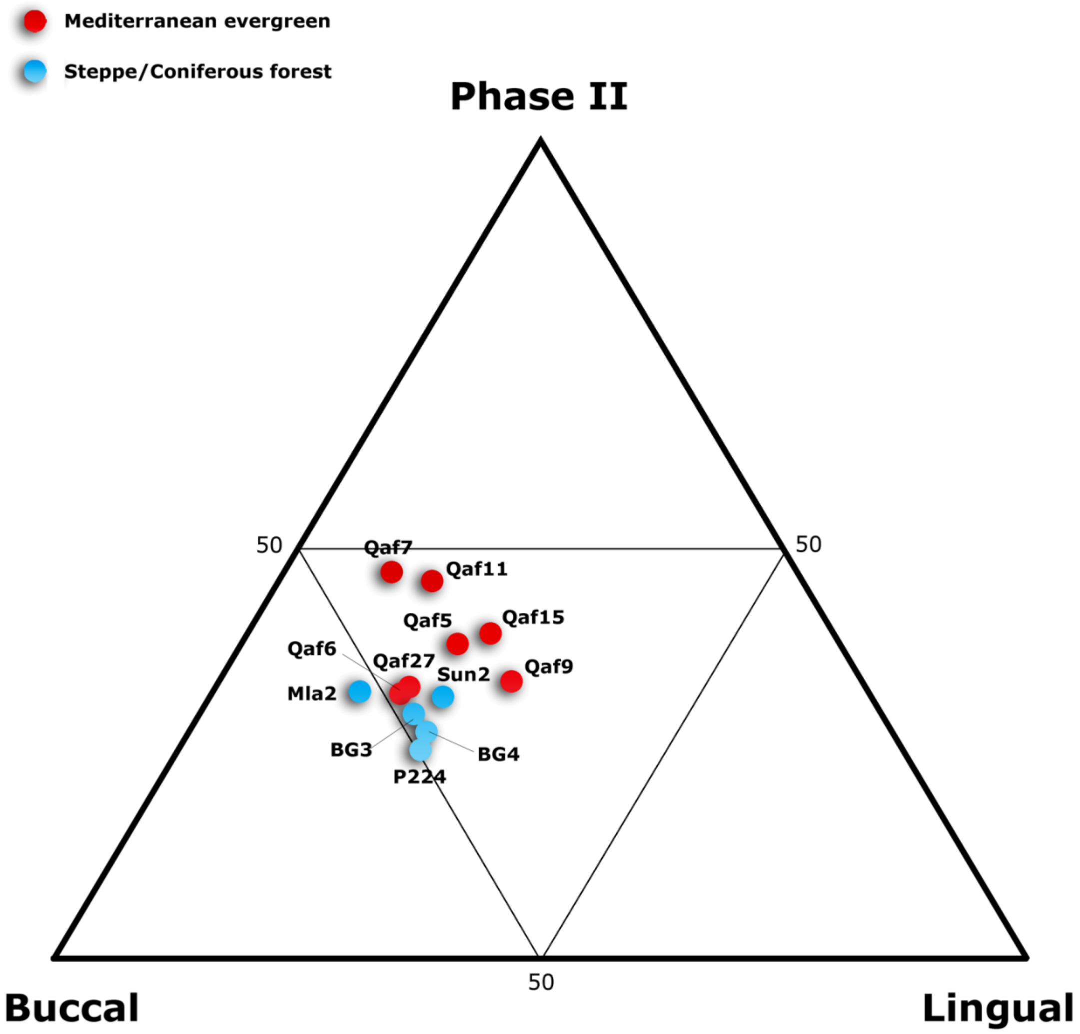


Figure 5.24 - Ternary plot based on the proportions of buccal, lingual and phase II facets, illustrating the distribution of the early *Homo sapiens* ecogeographic groups (Mediterranean evergreen and Steppe/Coniferous forest).

The SEHS show buccal phase I facets strongly developed (45.6 %), while in the MEHS are less prominent (39.9%). The lingual phase I facet are weakly pronounced in both groups (about 20%). Higher differences are found in the phase II facets which results to be prominent in the MEHS groups and less developed in the SEHS (see Appendix D, Tab. D28). The statistical comparison (Permutation *t* test) between the two EHS groups show *p* values statistically significant in the buccal phase I facets and in the phase II areas. The lingual phase I facets do not show any significant differentiation between MEHS and SEHS (see Appendix D, Tab. D29).

The ternary plot shows a clear separation between the two groups which slightly overlap due to the specimens Qafzeh 6 and 27, plotting close to the SEHS (Fig. 5.24). The statistical comparison between MEHS and SEHS based on the multivariate analysis (one-way NPMANOVA) displays a significant difference (see Appendix D, Tab. D30).

5.7.3 Dip angle

The buccal phase I facets show a lower inclination than those of NEA, especially evident in facet 1 and 1.1 which are characterized by dip angles lower than 20° and 10° respectively (Fig. 5.25). The lingual phase I facets results to be steeper, where facet 5 and 5.1 are the steepest facets of the whole occlusal wear area. The phase II facets display flatter areas with dip angles of about 20°. The protocone and hypocone tip crush areas are the flattest occlusal contacts (less than 10°).

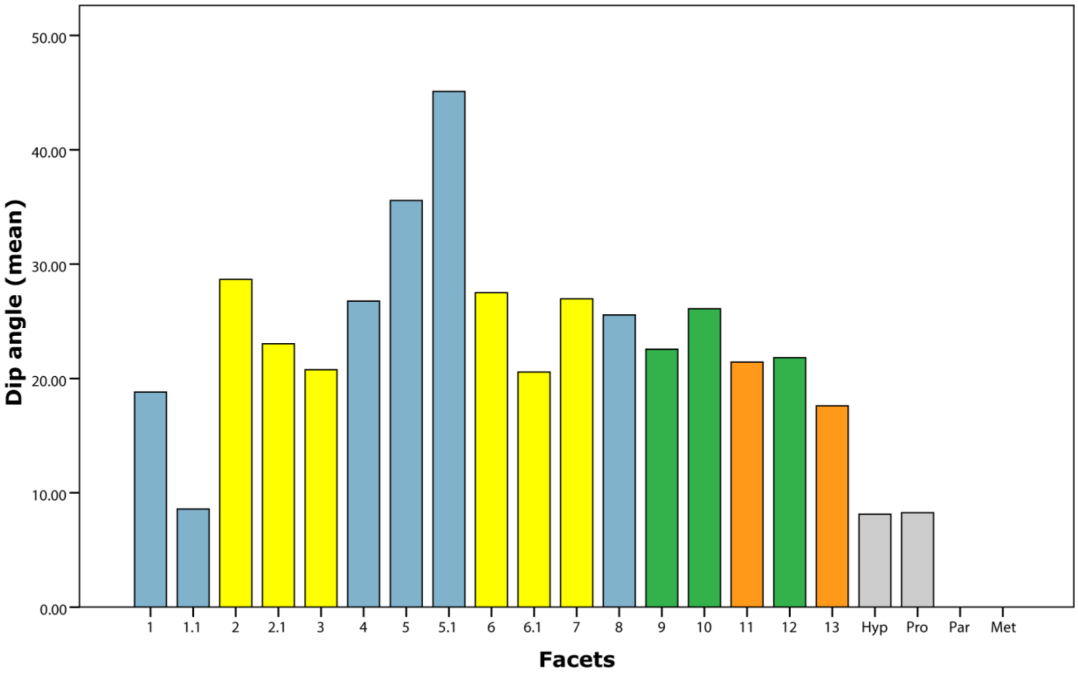


Figure 5.25 - Histogram presenting the mean dip angle of each wear facet within the early *Homo sapiens* sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange). Tip crush areas are in grey.

Considering the different degree of wear, the EHS groups would be constituted by only two MEHS specimens and two SEHS for wear stage 2 and by five MEHS and three SEHS for wear stage 3. Therefore, it is possible to carry out only a statistical comparison for the wear stage 3. The buccal phase I facets show an inclination of about 20° in both EHS groups. The MEHS possess lingual facets slightly steeper than those of the SEHS group.

The phase II facets instead have higher inclination in the SEHS. Considering all the wear facets the MESH group is characterized by dip angles slightly steeper than those of SEHS (see Appendix D, Tab. D31). The Permutation *t* test shows no statistically significant differences in each variable considered (buccal, lingual, phase II and total occlusal area) between the two EHS groups (see Appendix D, Tab. D32).

5.7.4 3D Occlusal Relief Index

As seen previously for the dip angle, the ORI values are affected by the degree of wear, and consequently will be only considered in the comparison between EHS specimens which show wear stage 3. The SEHS shows a higher ORI than the MEHS group (see Appendix D, Tab. D33), nevertheless the statistical comparison (Permutation *t* test) gives a not significant *p* value (see Appendix D, Tab. D34).

5.7.5 Dip direction

The phase I facets (both buccal and lingual) are characterized by two main dip directions pointing to a LRT and LPT movements (Fig 5.26). Although the difference between these two movements results to be quite clear, facet 1 and 1.1 show high values, closer to the LPT direction. The phase II facets are affected by the great overlap due to the facet 10 and 11.

The MEHS show LRT values similar to those of SEHS with higher standard deviation. The LPT facets in the MEHS groups are characterized by higher dip direction values with a lower standard deviation, indicating a more clear separation with the LRT facets (see Appendix D, Tab. D35). In the SEHS the dip direction point closer to the LRT compass area. The MPT and MT facets, in both the EHS groups, are characterized by similar directions which are uniformly distributed. The Watson-Williams test does not show any statistically significant difference between the two groups (see Appendix D, Tab. D36).

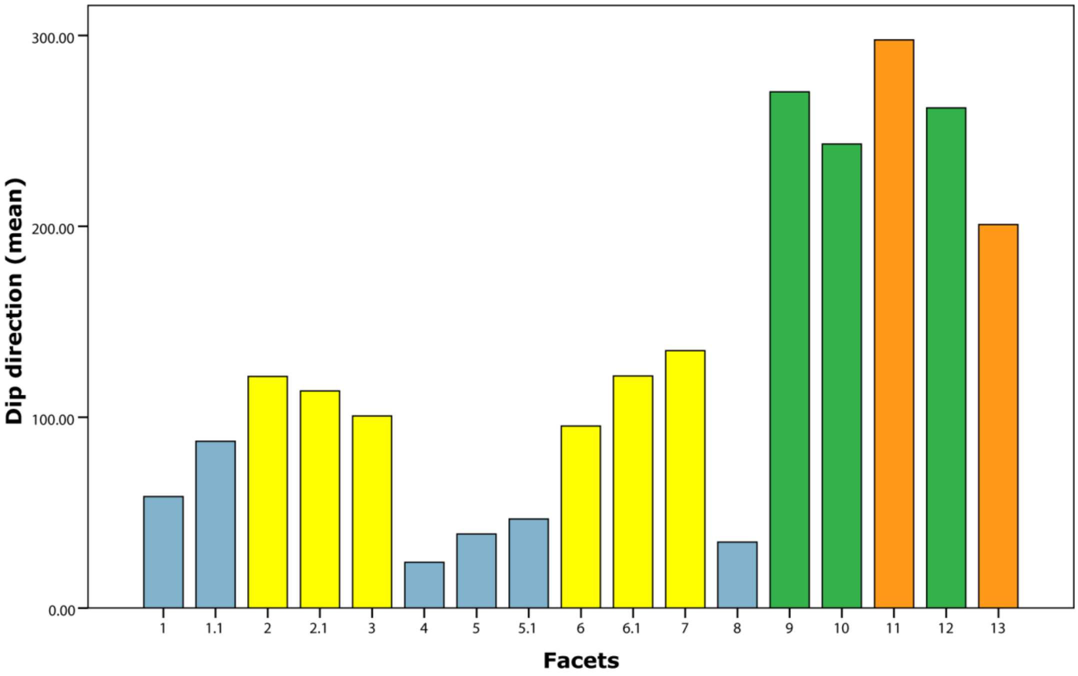


Figure 5.26 - Histogram displaying the dip directions (mean) of each wear facets within the early *Homo sapiens* sample. Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009): lateroretrusion (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange).

5.8 Comparison between Neanderthals, Early *Homo sapiens* and modern hunter-gatherers

The three groups, Neanderthals (NEA), early Homo sapiens (EHS) and modern hunter-gatherers (MHG) are constituted by 19, 12 and 42 specimens respectively.

5.8.1 Relative area

In the MHG group the buccal phase I facets are prominent, contributing to almost 50% of the total occlusal wear area, while in the NEA and EHS sample they are less developed (see Appendix D, Tab. D37). The statistical comparison (based on Mann-Withney U test) between the three different groups shows that the MHG result to be statistically different from the NEA and EHS (see Appendix D, Tab. D38). The lingual phase I facets are strongly developed in the NEA group, while in the EHS and MHG sample they are much less pronounced, representing about 20% of the occlusal surface (see Appendix D, Tab. D37). The statistical comparison reveals a significant difference between NEA and MHG and between EHS and MHG (see Appendix D, Tab. D38). The phase II occlusal areas show less pronounced differences between the three groups. The EHS group is characterized by well developed phase II facets which result to be less prominent (showing also similar values) in the MHG and NEA sample (see Appendix D, Tab. D37). The statistical comparison does not show any significance level between the three groups (see Appendix D, Tab. D38).

5.8.2 Tooth morphology

The relative area of the facets developed along the slopes of the same cusp have been summed, grouped and compared between MHG and fossil samples, in order to evaluate how the different tooth morphology which characterizes the different groups affects the occlusal wear pattern. The cusps of M^1 and M^2 have been considered separately.

1. Protocone: facet 5, 6, 9, 11, 13 and pro
2. Hypocone: facet 7, 8, 10, 12 and hyp
3. Metacone: facet 2, 2.1, 4 and met
4. Paracone: facet 1, 3 and par

In addition, since within the EHS sample is expected to find a different maxillary morphology between Middle Paleolithic and the Upper Paleolithic specimens (Bailey, 2002a, 2004, 2006), the EHS sample studied here has been divided in two smaller groups: Middle Paleolithic *Homo sapiens* (MPHS) and Upper Paleolithic *Homo sapiens* (UPHS). In the first upper molar of the Neanderthal group the degree of development of the wear facets follows the pattern PRO>HYP>MET>PAR, where the protocone results to be the most important occlusal area and the buccal cusps (metacone and paracone) represent the smallest areas, showing similar relative sizes (see Appendix D, Tab. D39). In the MPHS the pattern results to be similar to those of NEA. In the UPHS group a PRO>PAR>MET>HYP pattern is found. In general the protocone wear facets are less pronounced than those of NEA and MPHS, while the metacone occlusal area is well developed. In the modern sample a similar pattern than those of the UPHS is found. However, the MHG group, unlike of the UPHS, is characterized by a strong reduction of the hypocone occlusal area. A statistical comparison (based on the Pemutation *t* test) of the relative wear facet developed along the four main maxillary cusps between the different taxonomic groups have been applied (see Appendix D, Tab. D40). The hypocone wear areas do not show any significant difference between the groups. Similar results are obtained if the protocone occlusal area is considered. The analysis of the paracone wear facets displays difference statistically significant between NEA and MHG and close to the significance level between MPHS and MHG. The metacone occlusal areas do not show any significant difference between the taxonomic groups considered.

The comparison (descriptive) within the cusps of second upper molars takes into account only the NEA, MPHS and MHG groups, since no UPHS M^2 are present (see Appendix D, Tab. D41). In the NEA sample the PRO>PAR>HYP>MEA pattern is found, where the protocone occlusal areas result to be more prominent than those of first upper molars. The MPHS group is characterized by the same NEA pattern, however the protocone is not so pronounced and the hypocone and paracone occlusal area are more developed. The MHG sample is characterized by a strong reduction of the hypocone and by an increase of the protocone and metacone wear facets, determining a change in cusps pattern (PRO>PAR>MET>HYP). The statistical comparison has been carried out between the NEA and MHG samples, since the MPHS group is constituted by only two specimens. Statistically significant differences are found in the hypocone, paracone and metacone occlusal areas (see Appendix D, Tab. D42).

5.8.3 Dip angle

If we consider the wear stage 2, the inclination of the wear facets shows higher differences between the three groups than those obtained from the analysis of molars characterized by stage wear 3. Overall, the occlusal wear facets are relatively steeper in the NEA and EHS sample (27.7° and 28.1° respectively), while in the MHG are flatter (21°) (see Appendix D, Tab. D43). The buccal phase I facets are very steep in the NEA group (30.4°), showing a lower inclination in the EHS sample (25.9°), and flatter occlusal planes in the MHG group (22.3°). The lingual phase II facets display high dip angle values in the NEA and EHS sample (32.5° and 31.1° respectively), while in the MHG the inclination is much less pronounced (less than 20°). Finally, the phase II facets result to be flatter, but steeper in the EHS group. Using the Permutation *t* test it is possible to note a statistically significant difference between the mean inclination of the EHS and the MHG sample, while the difference between the NEA and MHG is close to the significance level (see Appendix D, Tab. D44). The inclination of the buccal facets is significantly different between the EHS and MHG group. The inclination of the lingual facets of the MHG group results to be statistically different with both NEA and EHS specimens. Last, the statistical comparison of the phase II facets does not show any difference between the three groups.

Analysing the facet inclination in the molars showing a wear stage 3, the differences between the groups seems to be less pronounced. Overall the dip angle is lower in the MHG group (see Appendix D, Tab. D45). The buccal phase I facets are steeper in NEA (24.6°) and flatter in EHS (20°) and MHG (18.9°). The lingual facets of the MHG and NEA group show similar values (about 21°), while in the EHS sample are steeper (27.9°). The phase II facets are flatter, slightly steeper in the NEA group. The statistical comparison highlights a significant difference in the buccal facets between the MHG and NEA group and close to the significance level in the lingual facets between the EHS and MHG sample (see Appendix D, Tab. D46).

5.8.4 3D Occlusal Relief Index

If specimens displaying a wear stage 2 are considered, the ORI results to be high in the EHS (1.63) and less pronounced in the MHG and NEA group (about 1.50 in both samples) (see Appendix D, Tab. D47). The statistical comparison (based on the Permutation *t* test) shows a significant difference between NEA and EHS and between EHS and MHG (see Appendix D, Tab. D48).

Considering molars with stage wear 3, the differences between the three groups are less evident. The MHG possesses slightly higher ORI values than the other two groups (see Appendix D, Tab. D49). The statistical comparison between NEA, EHS and MHG does not show any significant differences (see Appendix D, Tab. D50).

5.8.5 Dip direction

NEA and EHS show similar results regarding the LRT facets, while the MHG is characterized by higher values with an increase of the variability (see Appendix D, Tab. D51). A similarity between NEA and EHS is also found in the LPT facets, where the directions point more on the PT (protrusive) compass area. On the other side, the MHG group shows a higher variability with slightly lower LPT values. The MT facets are quite similar between all the three groups, where in the EHS sample the variability is reduced. The MPT facets result to be more similar between the NEA and MHG group, although the variability is much higher in the NEA. The EHS group shows lower MPT values. Using the Watson-Williams test, the statistical comparison of the dip direction between the three groups does not show any significant difference (see Appendix D, Tab. D52).

5.9 Comparison within the human fossil sample considering different vegetation areas

The fossil sample falls within three types of vegetation: deciduous woodland, Mediterranean evergreen and steppe/coniferous forest. The deciduous woodland group (DEW) is constituted only by the Krapina Neanderthals (12 specimens in total). The Mediterranean evergreen sample (MED) is composed by three Neanderthals (Amud 1, Tabun 1 and Shanidar 2) and seven EHS (Qafzeh). In the steppe/coniferous forest group (SFC) 9 specimens are included, four Neanderthals (Monsempron 2 and 3, Le Moustier 1 and Vindija V259) and five EHS (Barma Grande 3 and 4, Mladec 2, Sungir 2 and Pataud 224).

5.9.1 Relative area

The buccal phase I facets are more developed in the SCF group, while the DEW and MED show similar values (see Appendix D, Tab. D53). The results from the statistical comparison (Mann-Withney U test) indicate a significant difference between SCF and DEW and between MED and SCF (see Appendix D, Tab. D54). The lingual phase I facets instead result to be more pronounced in the DEW with equal values in the MED and SCF sample (see Appendix D, Tab. D53). The Mann-Withney U test confirms the descriptive analysis showing p values with a significance level between DEW and MED, and between DEW and SCF (see Appendix D, Tab. D54). The development of the phase II facets is more advanced in the MED sample, followed by the SCF and the DEW groups (see Appendix D, Tab. D53). The comparative analysis proves a statistically significant difference between DEW and MED, and between MED and SCF (see Appendix D, Tab. D54).

The graphical representation obtained using the ternary plot allows to discriminate between the three groups, where the DEW plot is in the direction of the lingual corner, the SCF specimens are distributed close to the buccal corner and the MED group is positioned in the central part of the graph directed toward the phase II corner (Fig. 5.27). However there is a slight overlap between the MED and DEW due to the Tabun 1 and Amud 1 specimens, while Qafzeh 6 and 27 (MED) plot between the SCF specimens.

The results obtained from one-way NPMANOVA analysis shows statistically significant differences in all the comparisons between the groups (see Appendix D, Tab. D55). The CVA scatter plot, which includes the projection of the original axes (biplot), reinforces the separation between the three groups, showing the importance of the three different axes (variables) for the discrimination (Fig. 5.28).

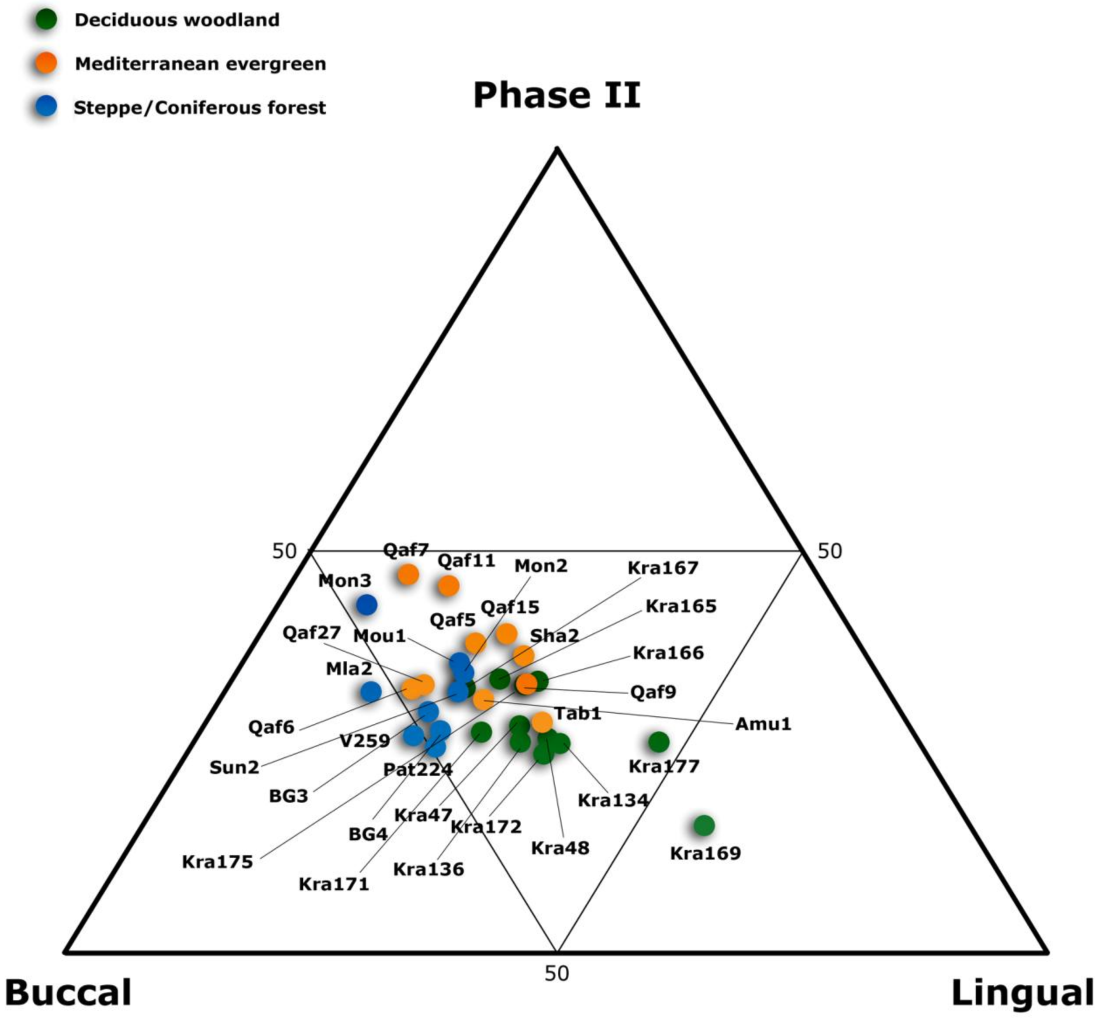


Figure 5.27 - Ternary plot illustrating the distribution within the fossil sample considering the proportions of buccal, lingual and phase II facets. The fossil sample was divided into three main groups taking into account the ecogeographic variation (Deciduous woodland, Mediterranean evergreen and Steppe/Coniferous forest).

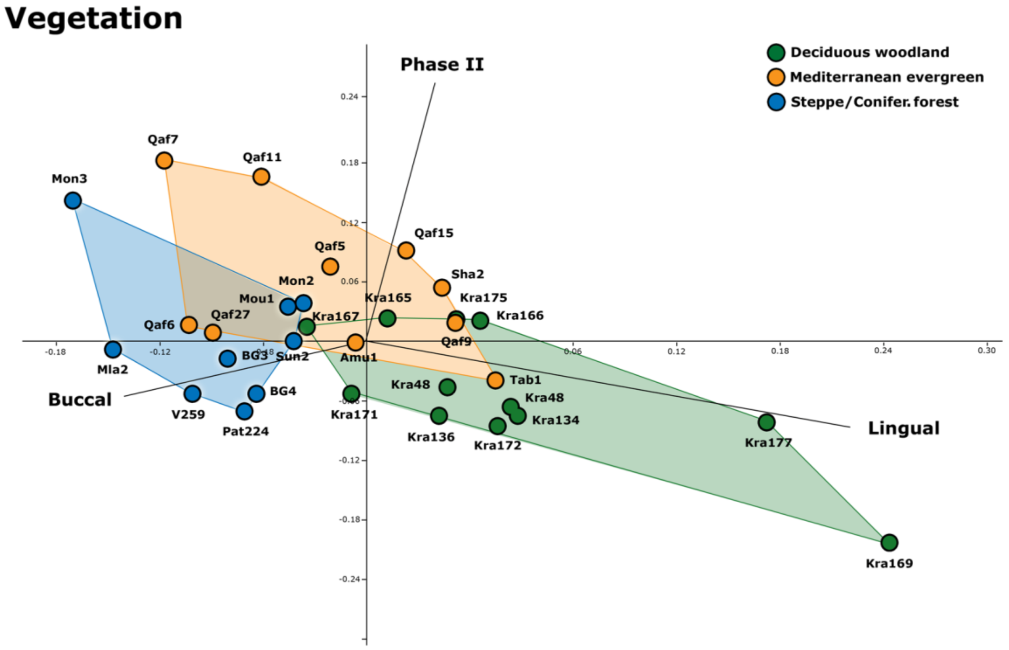


Figure 5.28 - CVA scatter plot (biplot) based on the relative areas of buccal, lingual and phase II facets, showing the distribution of the fossil sample taking into account the ecogeographic variation (Deciduous woodland, Mediterranean evergreen and Steppe/Coniferous forest).

5.9.2 Dip angle

Considering only the specimens with stage wear 2, the inclination of the buccal phase I facets show similar values in the three groups (between 27° and 28°). The lingual phase I facets are steeper in the DEW group (31°) and less pronounced in the MED (24°) and SCF (27°) sample (see Appendix D, Tab. D56). Conversely, in the phase II facets, the highest inclination is found in the SCF group (29°) and the lowest in the DEW sample (22°), while the MED show intermediate values (24°). Since the MED group is constituted only by two specimens it is not included in the comparative analysis. The comparison (Permutation *t* test) between DEW and SCF shows differences statistically significant in the lingual phase I facets and close to the significance level in the phase II facets (see Appendix D, Tab. D57).

Considering maxillary molars with wear stage 3, as the DEW sample is composed by only one specimen it will not be included in both descriptive and comparative statistical analysis (see Appendix D, Tab. D58). The differences between the MED and SCF groups are less pronounced than those seen between the same groups characterized by molars with wear stage 2. In all the four variables used (mean of the entire occlusal facet, buccal, lingual and phase II facets), there is only a slight difference between the two groups. Similar results are also obtained from the statistical comparison (Permutation *t* test) showing no significant differences between MED and SCF (see Appendix D, Tab. D59).

5.9.3 3D Occlusal Relief Index

Considering molars with wear stage 2, the ORI of the MED sample results to be the highest within the entire fossil group (see Appendix D, Tab. D60). However, since only two specimens constitute this group, a statistical comparison is precluded. Therefore, considering only the DEW and SCF, the Permutation *t* test does not show any statistically significant difference (see Appendix D, Tab. D61). Using specimens characterized by wear stage 3, the MED and SCF groups do not show any difference (see Appendix D, Tab. D62), as confirmed by the statistical comparison (see Appendix D, Tab. D63).

5.9.4 Dip direction

The DEW group is characterized by lower LRT values while the MED and the SCF sample possess similar LRT directions. The LPT facets show similar movements with a slight higher variability in the SCF sample. The MT and MPT facets display a great overlap (see Appendix D, Tab. D64). The Watson-Williams pairwise comparison does not show any statistically significant difference for each occlusal compass movement between the three groups (see Appendix D, Tab. D65).

5.10 Comparison of meat-eaters and mixed-diet hunter-gatherers with the fossil sample

The modern hunter-gatherers sample (MHG) is divided in meat-eaters (Inuit, Vancouver Islanders and Fuegians) and mixed-diet group (Australian aborigines and Bushmen), while for the fossil sample the vegetation groups are taken into account. Since the comparison of the dip angle and ORI requires the separation of the specimens with respect tothe two different wear stages, the fossil group would be strongly reduced, preventing the use of the statistical analysis. Therefore the dip angle and ORI will not be considered in this paragraph.

5.10.1 Relative area

The buccal phase I facets are strongly reduced in the DWN and MEN (about 38%) and more developed in the rest of the groups (between 45 and 48%). The lingual phase I facets are prominent in the DWN and MEN and less pronounced in other groups (see Appendix D, Tab. D66). However, the mixed-diet hunter-gatherers (MDHG) show more developed lingual wear facets (about 25%), which are more reduced in the SCN (18%) and in the meat-eaters hunter-gatherers (MEHG) where the lingual facets constitute only 15% of the total occlusal wear area. The phase II facets are more prominent in the MEHS (38%) and less developed in the DWN, SEHS and MDHG. The comparison between the different groups (Permutation *t* test) shows a statistically significant difference in the buccal phase I facets between the MEHG group on one hand and DWN, MEN and MEHS on the other hand (see Appendix D, Tab. D67). In addition, the comparative analysis of the buccal phase I facets displays differences statistically significant between DWN and MDHG and close to the significance level between MEN and MDHG. Considering the lingual phase I facets, statistically significant differences are found only comparing DWN and MEN with MEHG. A level close to the significance level is also found between DWN and MDHG. The statistical comparison between phase II facets of the different groups is less discriminatory. The only significant difference is found between MDHG and MEHS.

In the ternary plot the DWN group results to be separated from most of the rest of the sample pointing towards the lingual corner (Fig. 5.29). The MEN group is positioned in a central position, overlapping with the DWN and MEHS (which are pointing more towards the phase II corner). The SCN and SEHS plot separately from the other fossil sample, overlapping especially with the MEHG. Last, the MDHG overlaps (Australian aborigines) with the MEHG, but most of the group (Bushmen) results to be separated, plotting close to the DWN sample.

The multivariate analysis (one-way NPMANOVA) has been applied considering the Australian aborigines and Bushmen as two separated groups (see Appendix D, Tab. D68). Statistically significant differences are found between the DWN and MEHS and between the DWN and the MEHG. The differences obtained from the comparison between the MEHG and MEN and between SCN and MEHG are close to the significance level, as they are between Bushmen and MEHS.

The CVA scatter plot reflects the group distribution seen previously using the ternary plot, showing a clear separation of the DWN sample, which plots on the southeastern quadrant, overlapping with MEN (Amud 1 and Tabun 1) and slightly with two MEHG specimens (Fig. 5.30). The MEHS group plots on the central part of the graph (towards the positive values of the axis 2), overlapping with the MEN group and with the MEHG, caused by the specimens Qafzeh 6 and Qafzeh 27. The SCN and SEHS group, overlap each other, and with the MEHG sample (including the Australian aborigine specimens). The Bushmen plot between MEHG and DWN, slightly overlapping with the former group.

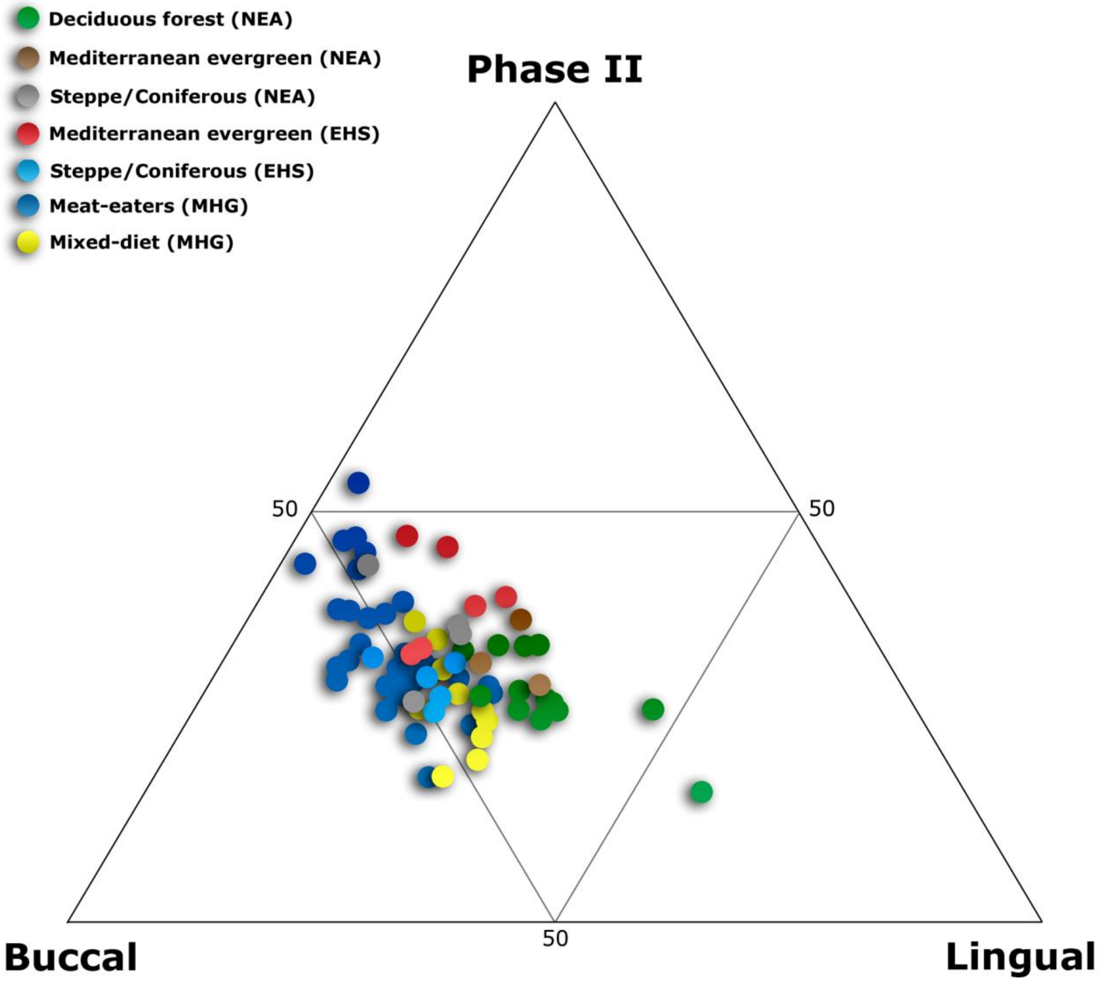


Figure 5.29 - Ternary plot based on the proportions of buccal, lingual and phase II facets, showing the distribution of modern hunter-gatherers (MHG), Neanderthals (NEA) and early *Homo sapiens* (EHS) groups (Deciduous woodland NEA, Mediterranean evergreen NEA, Steppe/Coniferous forest NEA, Mediterranean evergreen EHS, Steppe/Coniferous forest EHS, Meat-eaters MHG and Mixed-diet MHG).

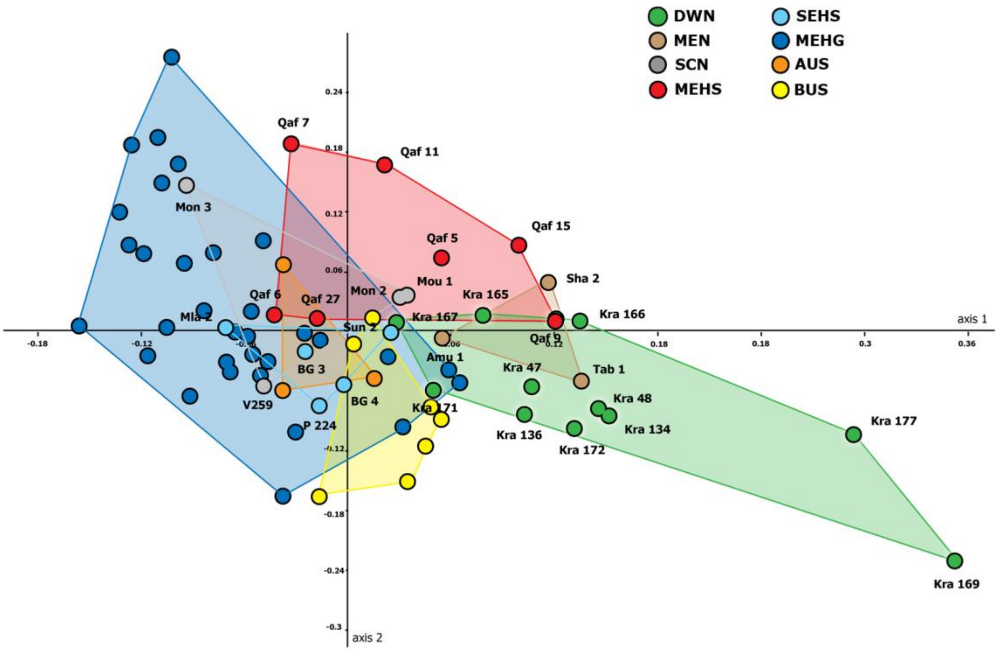


Figure 5.30 - CVA scatter plot illustrating the distribution of modern hunter-gatherers, Neanderthals and early *Homo sapiens* groups, taking into account the relative area of buccal, lingual and phase II facets. Groups: Deciduous woodland Neanderthals (DWN); Mediterranean evergreen Neanderthals (MEN); Steppe/Coniferous forest Neanderthals (SCN); Mediterranean evergreen early *Homo sapiens* (MEHS); Steppe/Coniferous forest early *Homo sapiens* (SEHS); Meat-eaters modern hunter-gatherers (MEHG); Australian aborigines (AUS); Bushmen (BUS).

5.10.2 Dip direction

The comparison of the dip direction does not show a clear difference between the groups considered in this analysis (see Appendix D, Tab. D69). As reported previously, the LRT and LPT facets differ between the MEHG and MDHG. However, regarding the fossil groups, a statistically significant difference is found only in the LRT facets between the DWN and MDHG, in the LPT facets between SEHS andMDHG and between SCN and SEHS, and in the MT facets between the DWN with the other two NEA groups (as seen before). The MPT facets do not show any statistically significant differences.

Chapter 6

Discussion

6.1 General Functional Aspects of the Occlusal Wear Pattern

6.1.1 Occlusal morphology

Best-fit plane inclination as calculated for individual occlusal wear facets are strongly related to the different functional demands necessary for processing food items during the chewing cycle. The "shearing" phase I facets (both buccal and lingual) display steeper planes than those of the "grinding" phase II facets, whereas "crushing" facet planes are seen to be the flattest areas of the entire occlusal surface.

Dip angles obtained from wear facet plane analysis shows that the inclination increases from the crushing areas to the phase II facets and from the phase II facets to the phase I facets. Differences in inclinations are likely due to different magnitudes of the forces exerted on the occlusal surface during the chewing cycle. The forces exerted on phase II facet wear surfaces generate a greater force than those exerted on the phase I facet surfaces. These results are concordant with the direction of forces generated by the varying masticatory movements/processes acting on ingested food during the chewing cycle phases. In fact, high magnitudes are expected from the forces directed perpendicularly to the contact plane such as those exerted during a crushing action. Lower magnitudes are expected from forces directed in parallel to the contact plane such as those exerted during a shearing action. The differences found in this study between phase I and phase II facets are in accordance with the results obtained by Krueger et al. (2008). These authors analyzed the dental microwear textures of three primate species differing in diet *(Alouatta palliata*, *Cebus apella*, and *Lophocebus albigena), and* suggested that the differences between phase I and phase II facets could be related to the angle of masticatory forces relative to the wear facet planes themselves.

However, the study of jaw movements in *Papio anubis* (Hylander & Crompton, 1980; Wall et al., 2006) showed that the occlusal load generated during phase II movements is insignificant.

This suggested that food breakdown during phase II occurs mostly at the end of phase I (crushing action) while the grinding activity of phase II is of minimal importance for food breakdown. Although from wear pattern analysis it cannot be determined if phase II facets are produced at the end of phase I or during phase II movements, the presence of flatter phase II than phase I areas indicates the involvement of prominent forces in creating such wear.

The phase I facets, as mentioned previously, are characterized by steeper facets than those of phase II. When combined with relatively vertical mandibular movement, this high inclination increases cutting efficiency which is necessary for shearing during phase I. Contrary to the description of Janis (1990), the lingual phase I facets are characterized by a well-defined shape similar to that of the buccal facets, showing a lower relative size than those of the buccal. Dip angle of buccal and lingual phase I facets show similar values while the lingual facets (5, and Carabelli facets 5.1 and 6.1) are seen to be the steepest wear areas of the entire occlusal surface.

Buccal and lingual phase I facet dip directions are similar although the lingual facet lateroprotrusive (LPT) movements show a slightly higher variation than those of the buccal facets primarily due to facet 7 which points in a more protrusive direction. These differences in LPT occlusal movements between lingual and buccal phase I facets could be related to the greater transverse jaw movements which characterize lingual facets (Janis, 1990). Tip crush wear facets are characterized by flatter areas, are more prominent on lingual cusps and normally enclose dentin exposures. The relative size of the crush area is similar to those of phase II facets with the exception of facet 9 which is larger. The development of tip crush areas is negligible for the metacone and paracone but more frequent in the protocone. The low frequency of tip crush identification is probably due to their tendency to coalesce with neighbour wear facets early during occlusal wear and facet formation.

6.1.2 Dental Occlusal Compass

Occlusal wear facet dip direction analysis shows that the vectors obtained are not distributed uniformly but are characterized by four main directions as predicted by the occlusal compass concept (Douglass & DeVreugd, 1997; Schulz 2003; Schulz & Winzen, 2004; Kullmer et al., 2004, 2009; Ulhaas et al., 2007). This result is more evident in LPT and lateroretrusive (LRT) facets where the directions are clearly distinct and separated. However, the occlusal movements responsible for phase II facet creation are not well identifiable. In fact, the mediotrusive (MT) and medioprotrusive (MPT) directions tend to overlap greatly and no comparative statistical analysis has shown any differentiation. Phase II movements are less rigidly constrained by tooth anatomy (Krueger et al., 2008); consequently it may occurs an increase of anisotropy, determining the overlap of the directions of the occlusal movements. However, most phase II movement overlap is created by facet 10 and 11, which, instead of pointing towards MT and MPT respectively, show the opposite situation. This result suggests that the occlusal movements responsible for the creation of facets 11 and 10 should be reconsidered including the mediotrusive component as a major direction for facet 11 (Kullmer et al., 2009), and the medioprotrusive component as major direction for facet 10.

6.1.3 Occlusal Relief

The 3D occlusal relief index decreases in the more advanced stages of wear. These results are similar to those obtained by M'Kirera & Ungar (2003) and Ulhaas et al. (2004) who show that occlusal relief in non-human primate teeth changes with wear. Occlusal relief does not depend only on the presence of steep facets as seen by the low coefficient of determination between ORI and mean dip angle but probably also depends on occlusal facet complexity where additional cusps and crests and the presence of numerous and tortuous grooves determine an increase in ORI.

6.1.4 Function of the Carabelli cusp

The Carabelli cusp shows a high frequency in the Neanderthal and early *Homo sapiens* groups (42.1% and 41.7 respectively), but is totally absent in our modern human sample. All specimens possessing the Carabelli trait show occlusal wear contacts (see Appendix C). Facets 5.1 and 6.1 are unique to the Carabelli cusp and show LRT and LPT movements respectively. Facet 5 often coalesces with facets 5.1 and 6.1 and therefore is the only facet commonly identified on the Carabelli cusp. Carabelli trait facets are characterized by steep planes which prove to be the most highly inclined of the entire occlusal surface. As suggested by Begg & Kesling (1977), the presence of the Carabelli trait increases in an advanced wear stage the available masticatory surface area, where lateral component predominance and steep contact planes indicate shearing action during mastication.

6.2 Relationship between Tooth Morphology and Occlusal Wear Pattern

The results obtained from the occlusal wear facet relative area analysis show that the Neanderthal group differs from the modern hunter-gatherers by possessing well-developed lingual phase I facets and a marked reduction in buccal phase I facets. The early *Homo sapiens* (EHS) sample is characterized by a reduction in buccal and lingual phase I facets and a slightly increase in phase II facets. In order to evaluate whether the differing between group occlusal wear patterns are due to different tooth morphologies, the relative cusp areas calculated by Bailey (2002a) were compared with the relative wear areas of the four main upper molar cusps (protocone, paracone, metacone, hypocone) (Fig 6.1). The Carabelli facets were not considered in this comparison.

The maxillary first upper molars of Neanderthals (NEA) are characterized by an enlarged hypocone, a reduced metacone and cusp pattern where PRO>PAR>HYP>MET (Bailey, 2002a, 2004, 2006; Gómez-Robles et al., 2007). The Middle Paleolithic *Homo sapiens* (MPHS) M^1s display a pattern similar to that of NEA where the hypocone is strongly developed and the metacone is reduced (Bailey, 2002a). The Upper Paleolithic *Homo sapiens* (UPHS) and modern *Homo sapiens* (MHS) are instead characterized by a cusp pattern where PRO>PAR>MET>HYP (Bailey, 2002a). However, the results obtained from the occlusal wear facet relative area analysis shows a different M^1 cusp pattern for NEA and MPHS where PRO>HYP>PAR>MET while in the UPHS and MHS the pattern is similar that found by Bailey (2002a). Protocone area proves to be the largest across all samples and in both analyses. However, the proportion of the protocones occlusal wear facets is significantly more than that obtained from the analysis of relative cusp areas. The hypocone wear facets, despite smaller relative size than cusp area, proves to be the second largest area in the NEA and MPHS first maxillary molars. The proportions of the paracones wear facets show results similar to those of the relative cusp areas although the difference between the NEA and MPHS group and the UPHS and MHS group are more marked. The metacone wear facets are less developed showing smaller differences than that seen in the relative cusp areas analysis.

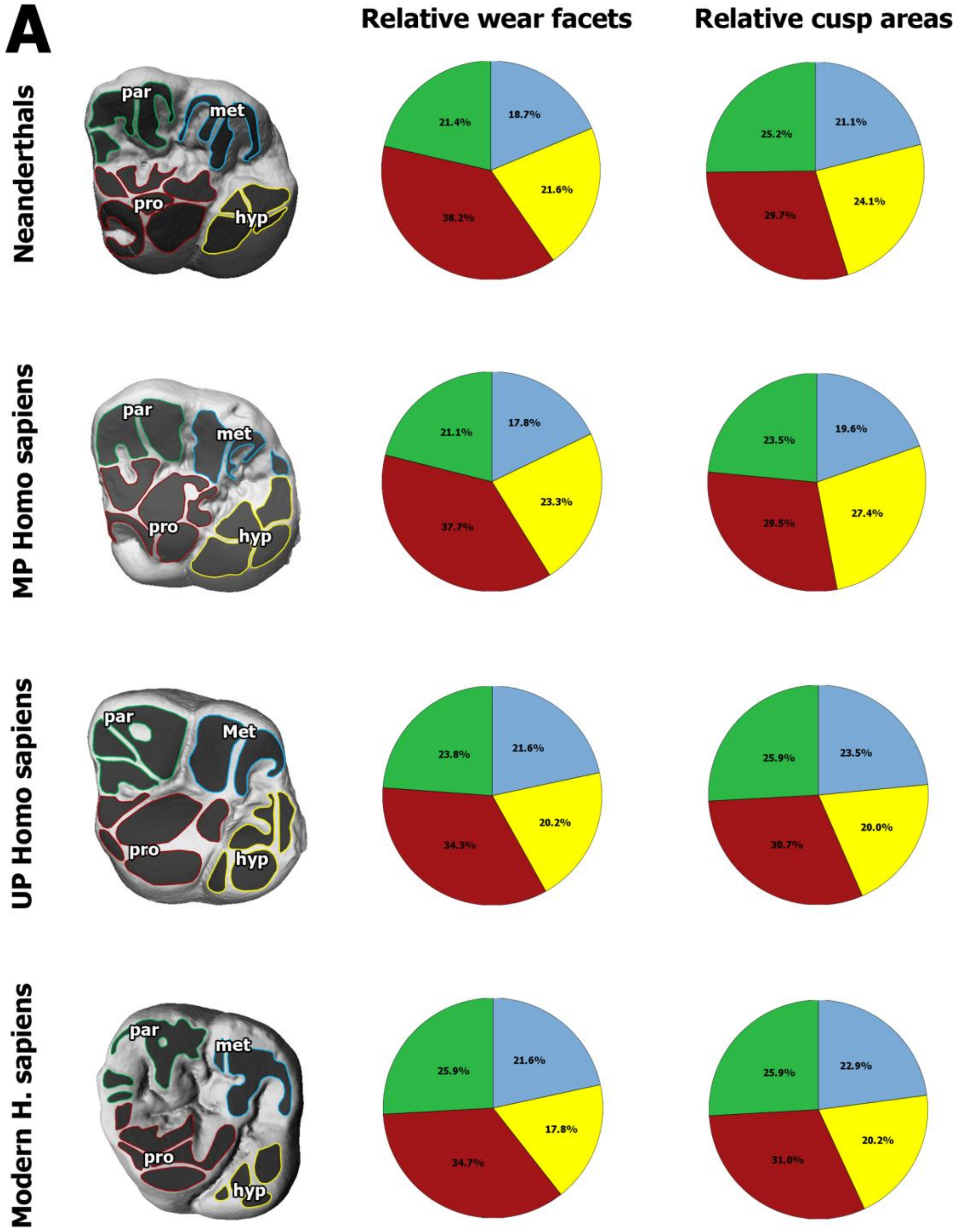


Figure 6.1 (A) – Continue –

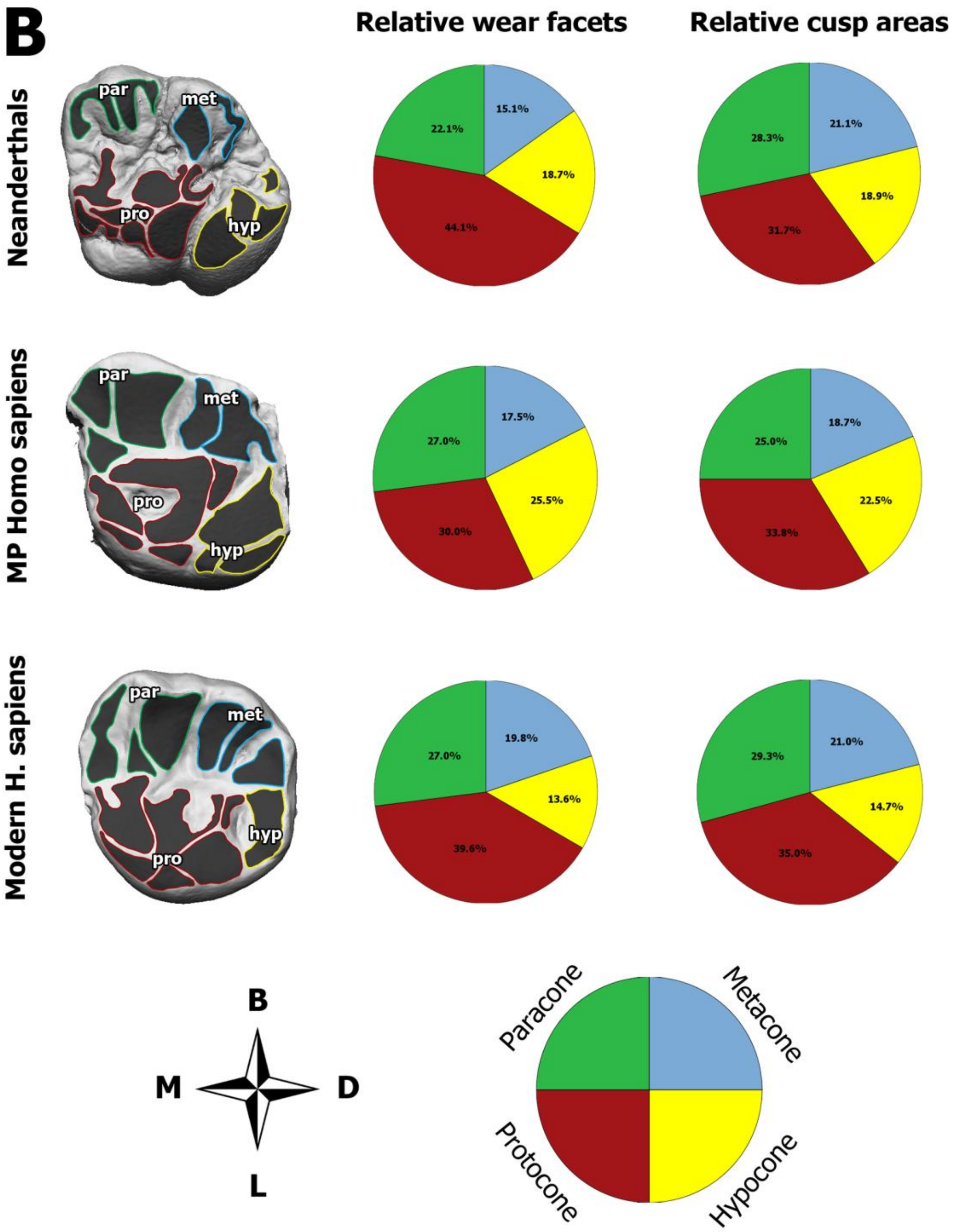


Figure 6.1 (B) - Comparison between relative facet areas and relative cusp areas in Neanderthals, Middle and Upper Paleolithic *Homo sapiens*, and Modern *Homo sapiens* M^1 (A) and M^2 (B). On the left, 3D polygonal models of maxillary molars indicating the four main cusps and corresponding wear facets. The pie chart in the centre is based on the relative facet areas which develop along the four main cusps. On the right, the pie chart represented is based on the relative cusp areas calculated by Bailey (2002a). Protocone (pro) in red; Paracone (par) in green; Hypocone (hyp) in yellow; metacone (met) in blue. Mesial (M); Buccal (B); Lingual (L); Distal (D).

The between group comparison of relative cusp areas shows a significant difference in hypocone and metacone areas between NEA and MHS (Bailey, 2002a). However, there are no significant differences between the hypocone and metacone cusps themselves. The only significant difference is found between the paracones of the NEA and MPHS group and MHS.

The pattern found in the NEA M^2 is PRO>PAR>MET>HYP which is shared by all the other groups with the exception of MPHS where the pattern is PRO>PAR>HYP>MET (Bailey, 2002a). Considering the wear facet relative areas, NEA and MPHS demonstrate a PRO>PAR>HYP>MET pattern, while the MHS group shows a PRO>PAR>MET>HYP pattern. The protocone is the most prominent occlusal area of M^2 although it is reduced in MPHS (although the sample size is very low n=2). The paracone wear facets of M^2 are more developed than those seen in M^1 while the metacone and hypocone wear facets are more reduced overall (in both M^1 and M^2). The M^2 relative cusp areas tend to be less distinctive showing no significant between group differences (Bailey, 2002a). However, wear facet comparisons between the NEA and MHS group show significant differences in the hypocone, paracone and metacone.

Taking into account the overall relative wear facet pattern (based on the relative wear facets), it is possible to see that intra-group variation is relatively high. For instance within the Neanderthal sample there is high variability in that Monsempron 2 and 3, Vindija V259 and Le Moustier 1, showing more similarities with the MHS sample than with the Krapina group.

The occlusal wear facets developed along the four main cusps tend to partially reflect the results obtained by Bailey (2002a) as shown by the presence of large NEA hypocone wear facets and the well developed MHS metacone facets.

However, the differences found between the first maxillary molars of NEA, MPHS, UPHS and MHS, tend to be less marked than those found by Bailey (2002a) in that they show no statistical significance level. In addition, unlike Bailey's results, hypocone, paracone and metacone M^2 facets are significantly different between the NEA and MHS group.

The results suggest that the level of occlusal wear facet differences which characterizes the different groups cannot be explained only by tooth morphology variation. In fact, the occlusal wear patterns show a high variation within a taxonomic group and a high degree of overlap between specimens belonging to different groups.

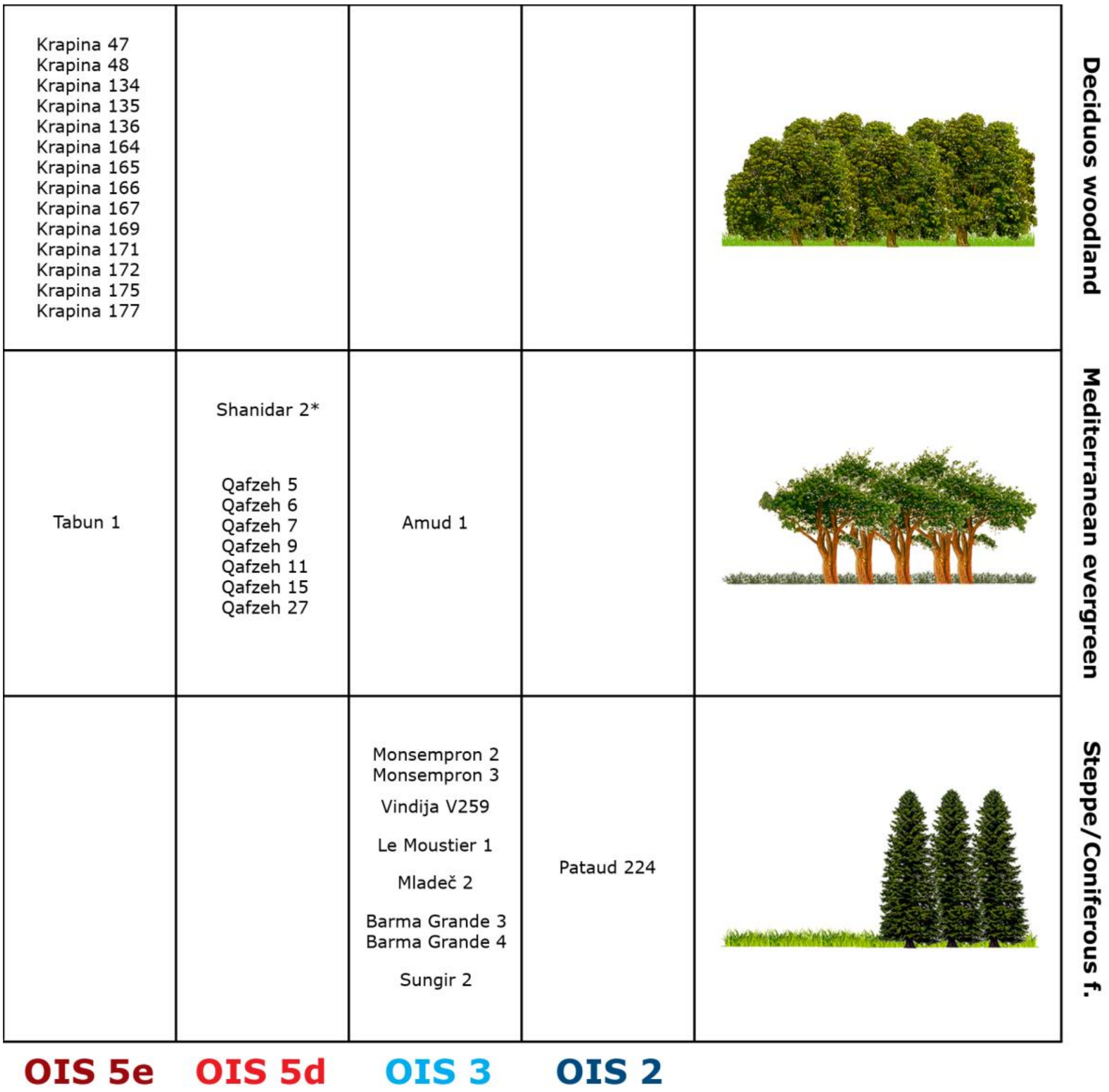
6.3 Ecogeographical variation within Neanderthals, early *Homo sapiens* and modern hunter-gatherers

The occlusal wear pattern of Neanderthals and early *Homo sapiens* (EHS), based on relative facet wear areas, follows a pattern of ecogeographical variation (Fig. 5.27 and 5.28). Specifically, specimens belonging to different taxonomic groups but who inhabited similar environments show corresponding wear patterns. However, within modern humans, this differentiation is less evident.

The Neanderthal and EHS samples are composed of specimens which occupied regions on the European continent and in the Near East during different chronological times. The alternation of glacial and interglacial cycles resulted in strong climatic changes with concomitant variability in local and regional ecozones. During cold phases, Europe was dominated by tundra in the north grading to open steppe and bordered by boreal forests while the Near East was coverd by dense forests (Hallin, 2002, 2008; Van Andel & Tzedakis, 1996). During warm phases, northern and central European environments were characterized by an increase in temperate, deciduous forests and by Mediterranean, evergreen vegetation in the southern latitudes while in the Near East, the climate was similar to that of present day conditions of Mediterranean semi-arid shrublands (Hallin, 2002, 2008; Van Andel & Tzedakis, 1996).

Studies of occlusal microwear demonstrated that Neanderthals were not characterized by only one type of wear pattern but showed a high variability which reflected their ecogeographical dispersion (Pérez-Pérez et al., 2003; El Zaatari, 2007). Buccal microwear analyses of Late Pleistocene European and Near Eastern hominids found a high variation in microwear pattern emphasizing the relationship between periodic climatic fluctuations rather than geographic dispersion where the specimens belonging to the warmer Oxygen Isotopic Stages (OIS) showed fewer striations than those from colder OIS (Pérez-Pérez et al., 2003). Unlike buccal microwear results, the analysis of Neanderthal microwear texture showed a pronounced correlation with different vegetation types where the specimens inhabiting cold, steppe environments differ from those from woodlands (El Zaatari, 2007). Within the woodland ecozone, three smaller groups have been further identified: coniferous forest, deciduous forest and Mediterranean woodland. The Upper Paleolithic *Homo sapiens* (UPHS) inhabiting coniferous woodlands including steppe elements were characterized by a wide variation in microwear surface texture complexity (El Zaatari, 2007).

The analysis of Neanderthal maxillary molar relative wear facet areas show a discrimination in occlusal wear patterns between different ecogeographical groups as seen in the dental microwear studies. The Neanderthal samples in this study are derived from three biomes: Mediterranean evergreen shrubland and woodland, deciduous woodland and steppe/coniferous forest.



OIS 5e	OIS 5d	OIS 3	OIS 2	
Krapina 47 Krapina 48 Krapina 134 Krapina 135 Krapina 136 Krapina 164 Krapina 165 Krapina 166 Krapina 167 Krapina 169 Krapina 171 Krapina 172 Krapina 175 Krapina 177				Deciduos woodland
Tabun 1	Shanidar 2* Qafzeh 5 Qafzeh 6 Qafzeh 7 Qafzeh 9 Qafzeh 11 Qafzeh 15 Qafzeh 27	Amud 1		Mediterranean evergreen
		Monsempron 2 Monsempron 3 Vindija V259 Le Moustier 1 Mladeč 2 Barma Grande 3 Barma Grande 4 Sungir 2	Pataud 224	Steppe/Coniferous f.

Figure 6.2 - Scheme illustrating Neanderthal and early *Homo sapiens* specimens grouped on the basis of Oxygen Isotopic Stages (OIS) and type of environment. * The specimen Shanidar 2 probably belongs to the period comprised between OIS 4 and 6 (Cowgill et al., 2007).

The Krapina sample (n= 12, OIS 5e), represents the deciduous woodland group while the specimen Amud 1 (OIS 3), Tabun 1 (OIS 5e) and Shanidar 2 (between OIS 4 and 5) constitute the Mediterranean evergreen group (n=3). The steppe/coniferous forest group (n=4) is comprised of specimens Monsempron 2 and 3 (OIS 4/ early OIS 3), Vindija V259 (OIS 3) and Le Moustier 1 (OIS 3). The EHS sample falls within two main biomes: Mediterranean evergreen and steppe/coniferous forest. The Qafzeh specimens (n=7, OIS 5d), constitute the Mediterranean group while the steppe/coniferous group (n=5) is composed ofthe specimens Mladeč 2 (OIS 3), Barma Grande 3 and 4 (OIS 3), Pataud 224 (OIS 2) and Sungir 2 (OIS 3) (Fig. 6.2).

Within the Neanderthal sample, the deciduous woodland group is characterized by high wear pattern variability (due mostly to specimens Krapina 169 and 177), reflecting the results obtained by El Zaatari (2007), who found high microwear texture variation in the deciduous forest Neanderthals. The occlusal wear pattern of the steppe/coniferous forest sample differs from those of the deciduous woodland and Mediterranean evergreen specimens, showing similar wear patterns, and thus are considered here as representing one homogenous ecozone group. El Zaatari (2007) found differences in microwear texture between Neanderthals which inhabited open environments (e.g. steppe) from those that lived in wooded areas. However, steppe and coniferous forest are characterized by similar climatic conditions with cold temperatures and low precipitation. This overall similar climate characteristic has probably affected the occlusal tooth wear of the steppe and coniferous forest Neanderthal specimens, determining a similar wear pattern.

Specimens from Mediterranean evergreen biomes display occlusal wear patterns similar to that of the deciduous forest group, but different from that of the steppe/coniferous forest environments. Within the Mediterranean group, Amud 1 is most closely related to the steppe/coniferous forest Neanderthals reflecting the cold and wet climatic conditions which characterized the Levantine territory during OIS 3, and indicating likely the increase of the vegetation cover (Hallin, 2002, 2008). Similar results were also found by El Zaatari (2007) where the microwear signatures placed Amud 1 with the European Neanderthals which inhabited deciduous forests. Tabun 1 wear pattern is very similar to those of Krapina and is confirmed by a level of surface complexity closer to the deciduous woodland Neanderthals (El Zaatari 2007).

The Monsempron specimens show high variation in occlusal wear pattern where Monsempron 3 is characterized by buccal phase I and phase II facets more prominent than Monsempron 2 which is more similar to Le Moustier 1.

Within the EHS sample, the Mediterranean evergreen group is clearly separated from the steppe/coniferous forest specimens with the exception of Qafzeh 6 and 27 who tend to be more closely related to the steppe/coniferous forest group than to the rest of the Levantine sample. The high variation in microwear texture in El Zaatari's (2007) UPHS was not found in the relative occlusal wear facet pattern in the Upper Paleolithic specimens of our sample which, albeit represents a rather homogenous group. While the Barma Grande specimens analyzed by El Zaatari (2007) showed heterogenous microwear textures, Barma Grande 3 and 4 included in our study display similar occlusal wear patterns.

The two EHS groups included in our sample, can also be separated based on distinctions in stone tool technology and also in some anatomical features (MPHS vs. UPHS). However, if the fossil specimens are not divided taxonomically and are grouped according to biome, the Neanderthals from steppe/coniferous forests cluster with the EHS of the same vegetation type. Neanderthals from Mediterranean areas share similarities with the EHS from the same environment but also with the Neanderthals from deciduous woodlands. Within the Mediterranean group, it is interesting to note that within the Neanderthal specimens, Shanidar 2 is most closely related to the Qafzeh sample. This result might suggest that Shanidar 2 lived in an environment where the climatic conditions were more arid than those of Amud 1 and Tabun 1.

If the modern *Homo sapiens* (MHS) sample is included in the comparison, the distinction between the different biomes becomes more complex and confused. Within the MHS sample it is possible to group together populations inhabiting the northern latitudes characterized by cold (but different) ecozones. However the Australian aborigines of semi-arid environments tend to be more closely related to the northern latitude populations rather than to the Bushmen who inhabited a similar arid biome. In addition, the Qafzeh group of the hot, dry Mediterranean Levant, show an occlusal wear pattern which strongly differs from the Bushmen. Despite that, both Neanderthals and EHS from steppe and coniferous forests display a wear pattern similar to modern hunter-gatherers inhabiting cold environments.

Considering only the Oxygen Isotopic Stages (OIS), the occlusal wear pattern shows high variability such that the Qafzeh and Krapina specimens plot separately although they belong to the same OIS. The differentiation between specimens from colder and warmer OIS is not evident which contrasts with the buccal microwear results obtained by Pérez-Pérez et al. (2003).

Taking into account the geographical area of each specimen, it is possible to identify the Near East group from occlusal wear pattern but the results are less clear within the European sample. For instance, the Vindija specimen is most closely related to Abri Pataud of southern

France instead of grouping with the Krapina sample which was collected only few kilometers distant from the Vindija Cave.

These results suggest that relative area occlusal wear pattern within the fossil sample is strongly related to the different types of biome which are then a factor of the spatiotemporal intersection of different geographical areas and OIS. The relationship between biome and occlusal wear pattern is also less evident in the MHS sample. Other factors such as specific cultural habits and differing food preparation techniques or lack of must be taken into consideration.

Due to the differences in wear facet inclination and 3D occlusal relief index (ORI) between molars with different degree of wear, the entire sample was divided in two groups comprising wear stages 2 and 3. This division further reduces the already small fossil sample size precluding a comparative analysis within the Neanderthal group. For the EHS sample using only maxillary molars in wear stage 3, the comparison between the Mediterranean and steppe/coniferous forest groups did not show any significant differences. Within the entire fossil sample, the deciduous forest and Mediterranean evergreen groups show wear facets slightly steeper than the steppe/coniferous forest specimens. This is especially evident in wear stage 2 maxillary molar lingual phase I & II facets. However, these differences vanish when wear stage 3 molars were considered. The comparison of the fossil sample ORI showed no between group differences for either wear stage 2 or 3 molars. Within the modern hunter gatherer sample, which is almost entirely composed of wear stage 3 maxillary molars, the comparison of dip angle and ORI did not differentiate between populations from any biome. These results indicate that the level of correlation between ecotype, and occlusal relief and wear facet inclination is lower and less clear than that seen using relative occlusal wear areas. Using the wear facet dip direction, the overall picture becomes even more complex. The mediotrusive (MT) and medioprotrusive (MPT) wear facets are rather similar, however, it is not clear if facets 11 and 10 should be considered MPT and MT facets respectively. Within the Neanderthal sample, the deciduous forest group shows a higher variation in lateroprotrusive (LPT) and lateroretrusive (LRT) facets than those of the steppe/coniferous forest environments. In the EHS sample, the mediterannean group is characterized by a higher variability in LRT facets and lower in LPT facets than those of the steppe and coniferous forest environments. Taking into account the entire fossil sample, the relation between dip direction and biome decreases strongly. In fact, while the Mediterranean evergreen and deciduous forest groups show a higher variation in the LRT facets than those of the steppe/coniferous forest environments, the latter group displays the highest variability in the

LPT facets. The statistical comparison of dip direction did not show any significant difference either within group nor between groups. In contrast, within the MHS sample, differences were found in LPT and LRT facets between the specimens inhabiting semi-arid environments and those coming from cold climates. However, LRT variation is higher within the semi-arid group whereas the LPT variation is more pronounced in the cold environment group.

The results obtained from the analysis of the facet dip directions are contradictory showing only minimal differentiation between different biome types. Therefore, dip directions cannot be considered useful in separating out the different groups based on biome alone.

6.4 Diet reconstruction derived from occlusal wear pattern analysis

Human populations consuming different food materials, show clear differences in the occlusal wear pattern. A high consumption of animal proteins appears to be related to an increase in the development of the buccal phase I facets, whereas an increase of the lingual phase I facets seems to be related to the addition of plants to the daily diet.

6.4.1 Diet in the modern hunter-gatherers

The analysis of the occlusal wear pattern of the modern hunter-gatherer molars, based on their relative areas, allows us to differentiate the "carnivorous" populations from those who are dependent on a mixed diet (Fig. 5.12 and 5.13). Inuit, Vancouver Islanders and Fuegians are characterized by a different wear pattern from those of the Bushmen. The Australian aborigines, who represent the most closely related group within the modern hunter-gatherers sample to the Bushmen, also show many similarities with meat-eater populations. This result reflects the importance of the plant materials in the Australian aborigines' subsistence albeit supplementary, considering their primary consumption of animal proteins (Brand-Miller & Holt, 1998).

A strong development of the buccal phase I facets occurs in the meat-eater populations, compensated by a marked reduction of the lingual phase I facets. On the contrary, in the mixed-diet hunter-gatherers the lingual facets tend to be more pronounced than those of the meat-eaters. The phase II areas are less distinctive, although there is a significant difference between Inuit and Bushmen - being more prominent in the former. Contrary to the results obtained by Gordon (1982), Teaford & Walker (1984) and Krueger et al. (2008), who claimed the importance of the microwear patterns on phase II facets better distinguished taxa with differing diet than do those on phase I facets, in our analysis the relative areas of phase I facets hold more information about food composition than phase II facets. From here it is possible to separate the meat-eaters from the mixed-diet hunter-gatherers. Janis (1990), in analyzing the wear pattern of three *Colobus* species depending on different diet, found that the phase I facets and the crushing wear (produced mostly during puncture-crushing), were significantly more distinctive than phase II facets. The difference in the importance of phase I or phase II facets in discerning animal dietary habits more accurately, could simply reflect the detail level used to analyze the tooth wear (macrowear vs. microwear).

The mastication of food items with different physical properties, such as abrasiveness, toughness, hardness and brittleness, requires different masticatory forces and processes. Meat is a tough, fibrous foodstuff with low-abrasiveness (Popowics & Fortelius, 1997; El Zaatari, 2007). The texture of plant materials is extremely variable, even within the same species. In fact, the different anatomical parts of the plant can show different physical properties.

Buds, flowers and shoots are usually soft, while the veins and stems of leaves, seeds and roots, represent a tougher material (Teaford & Ungar, 2000). Additionally, many plants have silica phytoliths, which renders them a highly abrasive food type. In order to breakdown meat and leaves (which are a tough and pliant food source), a shearing masticatory process is required. In many grazing and browsing herbivores, and in the carnassial teeth of carnivores, the posterior dentition is characterized by the presence of sharp cusps, which represent a morphological adaption to better process this particular type of food (Luke & Lucas, 1983). Human dentition however, is characterized by low-cusped teeth, which have adapted to an omnivorous diet, mainly constituted of brittle and fairly hard foods (Luke & Lucas, 1983). The high consumption of meat in the modern hunter-gatherers is related to the extension of the buccal phase I facets (shearing) as suggested by Janis (1990) who analyzed the occlusal wear of a wide variety of living herbivores, concluding its association with the division of tough, fibrous and flat food items. Although herbivores are characterized by a totally different tooth morphology than modern humans, the concomitant presence of large buccal phase I facets in non-human primates, with a diet rich in tough and fibrous food (Janis, 1990), highlights the importance of these occlusal areas for processing pliant, tough food, regardless of the taxonomic affiliation. In the Australian aborigines and Bushmen, there is a decrease in the amount of buccal phase I facets (more evident in the Bushmen), which is compensated by an increase of the lingual phase I facets. The extension of lingual phase I facets in the modern hunter-gatherer group, seems to be related to the progressive increase in the consumption of hard and abrasive foodstuffs, including roots, seeds, gums and probably other plant materials. In fact, in the Australian aborigines (whose diet contains a larger proportion of vegetables than those of the meat-eaters), lingual wear facets are more developed than those of the Inuit, Vancouver Islanders and Fuegians. The Bushmen, who consume the greatest amount of plant materials in the entire modern human sample, show the largest lingual phase I facets. The presence of large lingual contact areas may indicate an increase of the transverse component of the jaw movements (Janis, 1990), which would be necessary for the comminution of the plant food. These results are in accordance to those obtained by Janis (1990), wherein herbivorous mammals with an omnivorous diet show more pronounced lingual phase I facets than those of browsers and grazers. Janis (1990) also suggested that the increase of the lingual phase I facets found in the living ungulates, could be related to the ingestion of softer food items such as fruit. The phase II facets are more developed in the meat-eaters group and Australian aborigines, than those of the Bushmen. This result is contradictory to those found by Janis (1990), where increases of the phase II facets were associated with a more frugivore dietary type. It is possible the increase of the phase II areas was related to a decrease of the lingual phase I facets.

Within each hunter-gatherers group the occlusal wear patterns result to be quite variable. The high variation is especially evident in the Vancouver Islanders and Fuegians, and less in the Australian aborigines (with only three specimens), Bushmen and Inuit. The variability in the occlusal wear pattern could be related to the exploitation of different food sources. In fact, the modern hunter-gatherer sample used in this analysis is composed of specimens collected from different geographical places at different periods in time. This variability within the sample could reflect the exploitation of different food sources, determining the degree of heterogeneousness of the occlusal wear pattern in the different groups. Within the Inuit sample, the specimens coming from the western coast of Greenland (FC 810, FC 833-2 and FC 833-3) and from the eastern coast of Canada (FC 826) are characterized by a wear pattern with a high degree of similarity. All these specimens occupied a similar geographical area, localized along the western and eastern cost of Baffin Bay, which probably provided similar food sources. The specimen BD1191, who is probably an Ipiutak from the western coast of Alaska, shows an occlusal wear pattern which differs from those of the Greenlander specimens. However, the specimen FC 833 localized in the eastern coast of Baffin Bay, and the specimen FC 857 from Greenland, both show a different occlusal wear pattern than those of the other "Baffin Bay" specimens. In the Fuegians the situation is less clear. The only Fuegian specimens who can be grouped together (AM 80968 and NHMW 6035, since they appear to belong to the Ona tribe), show a different occlusal wear pattern. The Vancouver Islanders represent further variability in the group. This is probably related to the large sample size (N=15), and by the presence of individuals belonging to various tribes, which were characterized by a consumption of different food sources. In the Bushmen sample, specimens S5, S7, S9 and S17, which belong to the Hottentots tribe, show a similar wear pattern (with the exception of S19), whereas the specimen S16, belonging to the "true" Bushmen tribe, is characterized by a different wear pattern. However, the results of specimen S1, who also belongs to the Bushmen, are more similar to the Hottentots.

The usefulness of the dental microwear analysis of a heterogeneous modern hunter-gatherer sample, used as a comparative database for fossil specimens, has been brought into question by El Zaatari (2007). The author, in particular, refers to the modern human sample used by Lalueza et al. (1996), who compared the buccal microwear of different modern hunter-gatherers with Pleistocene hominids, defining it "certainly unsuitable" for this type of analysis. The Fuegians sample has been especially criticized since it was composed of the Ona, who relied on the consumption of terrestrial mammals (such as the guanaco) and the Yahgan, who relied mostly on marine food sources. Lalueza et al. (1996) assumed that, since the Yahgan and Ona are closely related, they probably had a similar diet. El Zaatari (2007) argued that this type of assumption is inappropriate and only a modern human sample with adequate information on their location, attribution, date and dietary habits should be analyzed. Although having a homogenous group with detailed information would certainly have improved the analysis and made it more reliable, it is dubious to think that close populations who relied on the consumption of food sources with slight differences in toughness and fibrousness would have a microwear and macrowear pattern so considerably different. Furlong (1917) described that in part the Ona's food supply was the same as that of the Yahgan.

As the results have shown, hunter-gatherers who relied on the exploitation of different food sources present also a varying occlusal wear. The same type of results were only in part obtained by El Zaatari (2007), where the Aleutian Islanders (who relied heavily on the consumption of meat) show a surface complexity similar to those of the Khoe-San (Bushmen), where up to 80% of the diet was composed of plant materials (Silberbauer, 1981). It is therefore evident that the relatively small differentiation between human populations living in similar environments, and who may have similar dietary habits is not fundamental in describing the occlusal wear pattern. In fact, as the same El Zaatari (2007) claimed, it was not possible to distinguish marine and terrestrial diet from the dental microwear pattern.

In considering the inclination of the wear facets, no significant distinction was found between groups differing in diet. The Australian aborigines are characterized by having the flattest occlusal surface within the entire modern human sample. This result could reflect the introduction of abrasive food items such as roots, tubers and other plant materials into their diet. The meat-eater hunter-gatherers show wear facets steeper than those of Australian aborigines, reflecting the less abrasive nature of meat. However, the Bushmen who consumed a larger quantity of vegetables than the Australian aboriginal sample also show wear facets characterized by a higher inclination – even higher than those of the meat-eaters. This result suggests that external factors other than the food items ingested, affect the occlusal wear, and in particular the inclination of the wear facets.

The occlusal relief found in the modern hunter-gatherer groups, similar to the results obtained for wear facet inclination, show little difference between the meat-eaters and mixed-diet groups. The only two groups characterized by slightly different occlusal relief indexes (ORI) are the Australian aborigines with low ORI, and the Inuit with a higher ORI. As previously suggested with the wear facet inclination, the ORI is the result of the abrasiveness of the daily diet of the different hunter-gatherer groups and the presence of associated external factors.

The lateroretrusive (LRT) and lateroprotrusive (LPT) facets of mixed-diet hunter-gatherers differentiate them from the meat-eater groups. In the LRT facets of the mixed-diet hunter-gatherers the laterotrusive (LT) component is more prominent, while in the meat-eaters group the LRT facets point more in the retrusive (RT) direction. The LPT facets of the mixed-diet hunter-gatherers are characterized by a pronounced protrusive (PT) component, while in the meat-eaters this is more laterotrusive. Overall the mixed-diet hunter-gatherers show a wider range of occlusal movements between the LRT and LPT facets than those of the meat-eaters group. This result is probably in relation to the introduction of plant materials into the daily diet, which requires a wider phase I jaw movement in order to process and reduce to smaller parts prior to swallowing. The phase II occlusal movements (mediotrusion (MT) and medioprotrusion (MPT)), as seen previously are not distinguishable between groups differing in diet.

However, the meat-eater hunter-gatherers show a higher variability in occlusal movements than those of the mixed-diet group. This result is not in relation with the hypothesis that exploitation of a high diversity of food would create a highly variable wear pattern. The different sample size which characterizes the two modern human groups may explain this difference. It is most likely taht the flatter occlusal surface of the meat-eaters compared to those of the mixed-diet populations (with the exception of the Australian aborigines), determines an increase of the possible jaw movements during mastication.

Thus, the dentition of the meat-eaters group is released by the occlusal constraints, allowing a greater range of possible movements during the chewing cycle. In fact, taking into account the dip directions found in the Bushmen group, who show the steepest wear facets within the entire modern human sample, this variability proves to be lower than those found in the meat-eater hunter-gatherers. Therefore, the variability of the occlusal movements seems to depend more on the occlusal morphology than on the type and diversity of food ingested.

6.4.2 Reconstruction of the diet of Neanderthals and early Homo sapiens

Dietary reconstruction based on the composition of the faunal assemblage and lithic industry (e.g. Patou-Matis, 2000; Burke, 2004; Hockett & Haws, 2005), stable isotope analysis (Fizet et al., 1995; Bocherens et al., 1999, 2001, 2005; Richards et al., 2000, 2008; Drucker & Bocherens, 2004; Beauval et al., 2006), and dental buccal microwear studies (Lalueza et al., 1996), point out that the Neanderthals were active hunters feeding mostly on the meat of large and medium-sized herbivores. However, the methods used for the reconstruction of the Neanderthal diet, as seen above, are characterized by some limitations. In particular, the bone preservation is more effective than those of plant remains, giving the impression that meat was the primary food source (Mann, 1981). For this reason, the study of archaeological records tends to underestimate plant consumption and to overestimate animal consumption (Hastorf, 1988).

Isotopic studies of bone collagen (which is largely composed of protein) reflect the dietary protein consumed but do not indicate the bulk diet (Gannes et al., 1997). As animal sources are high in protein, they will be overrepresented in bone collagen at the expense of plant food which contains a low percentage of proteins (Sponheimer & Thorp, 2007). Additionally, since stable isotope analyses have only been applied to thirteen Neanderthal adults coming from cold and steppic environments of central and northern Europe, it is necessary to increase the sample size, especially including specimens who inhabited warmer environments from different geographical areas, in order to obtain a complete picture of the Neanderthal subsistence.

Lastly, as pointed out by Pérez-Pérez et al. (2003), the buccal microwear patterns of the fossil sample studied do not match those of the comparative modern human populations.

The eco-geographical differentiation in the occlusal wear pattern (based on the analysis of the relative facet areas) seen within the Neanderthal (Fig. 5.18 and 5.19) and early *Homo sapiens* (EHS) (Fig. 5.24) sample is the result of the exploitation of different food sources. In cold environments (steppe and coniferous forest), Neanderthals and EHS show an occlusal wear pattern similar to those of the modern hunter-gatherers with a high consumption of animal proteins. The Neanderthals who inhabited the Mediterranean and deciduous woodland environments are clearly distinguished from the meat-eater hunter-gatherers, showing more similarities with the mixed-diet group. Finally, the EHS from the Mediterranean environments are equally differentiated from the highly carnivorous hunter-gatherers and also from those who consumed a large quantity of plant materials, while showing similarity to the Australian aborigines, who relied on a diet mostly composed of meat but which also included plant food. The Neanderthals from the deciduous forest environments (DWN) show a variable occlusal wear pattern characterized by a strong development of the lingual phase I facets and a reduction of the buccal phase I facets. The high variability in occlusal wear, as suggested by El Zaatari (2007), could reflect the exploitation of a high diversity food sources (plants and animals) available in these types of environments. The reduction of the buccal phase I facets may be related to the reduction in the consumption of fibrous and tough food (such as meat), while the increase of the lingual phase I facets may be related to the introduction of hard and abrasive food (such as plant materials) into the daily diet. The analysis of the faunal remains and stone tools found at the Krapina site, has suggested the exploitation of large game, including the Merk's rhinoceros (Miracle, 1999). The discovery of cutmarks on the human skeletal remains of the Krapina site, led some authors to hypothesize that Neanderthals were cannibals (e.g., Gorjanovic-Kramberger 1906; Smith 1976; White 2001). However, the cannibalism hypothesis is contestable (Karavanić, 2004) as the human bodies could have been defleshed in preparation for burial (Trinkaus, 1985; Russel, 1987).

As discussed above, the reconstruction of the diet cannot be based on the faunal assemblage alone. If Neanderthals relied on the exploitation of animal food sources only, one would expect an occlusal wear pattern very similar to those of the Inuit, Fuegians and Vancouver Islanders. However, the occlusal wear pattern in the DWN group clearly differs from the meat-eater modern humans and Australian aborigines. The occlusal wear pattern of the DWN also differs from those of the Bushmen, showing more developed lingual phase I facets (Fig. 5.29 and 5.30). This result could simply suggest a diet high in vegetable materials, where the exploitation of plant food was more prominent than those of Bushmen. However this assumption cannot be confirmed since no hunter-gatherers that rely on a complete vegetarian diet have been included in the comparative analysis. Moreover, the development of the occlusal wear pattern is also affected by the tooth morphology as seen previously. Therefore, the stronger development of the lingual phase I facets of the DWN compared to those of Bushmen could also be related to the enlargement of the hypocone cusp which characterize the Neanderthal upper molars (Bailey, 2002).

The Neanderthals from the Mediterranean environments (MEN) show an occlusal wear pattern similar to those of the DWN, with well developed lingual phase I facets and less prominent buccal phase I facets. These results suggest that the MEN relied on a broad dietary spectrum, including the consumption of animal proteins and plant foods. In fact, as seen with the DWN, the occlusal wear pattern of the MEN appears to be different from those of the meat-eater modern humans, showing more similarities with those of the Bushmen and Australian aborigines. Similar results were also obtained from dental microwear texture analysis (El Zaatari, 2007), where the specimens Amud 1, Kebara 2 and Tabun 1 show a wear pattern similar to the Neanderthals who occupied the deciduous forest of southern Europe, and similar to those of the Khoe-San hunter-gatherers (Bushmen). However, the comparison of the buccal microwear between modern hunter-gatherers and Pleistocene hominids, have led some to hypothesize that the specimens Tabun 1 and Amud 1 had a carnivorous diet (Lalueza et al., 1996). In particular, Pérez-Pérez et al. (2003) suggested that the buccal wear pattern of the specimens who inhabited warm environments (such as Amud 1), indicate the exploitation of a low-abrasive diet, probably more meat dependent. However, the consumption of a low-diversity diet (mainly consisting of animal proteins) in a warm environment (such as the Mediterranean evergreen) paired with the availability of a high-diversity of food sources, is contradictory. In addition, the finding of numerous plant fossils in the cave deposit in Amud (Madella et al., 2002) and Kebara (Albert et al., 2000; Lev et al., 2005), some of which edible, indicate that the Neanderthals ate a wide variety of food items, including plant materials such as legumes, wild grasses, fruits and seeds. This new evidence is in contradiction to the results obtained from the buccal microwear analysis (Lalueza et al., 1996; Pérez-Pérez et al., 2003), supporting the results obtained in our analysis and those obtained from the dental microwear texture (El Zaatari, 2007). Recently, microfossil plants trapped in the dental calculus of the specimen Shanidar 3, have presented the first direct evidence of the intake of plant materials (such as starch grain from grasses) in the Neanderthal diet (Henry & Piperno, 2008). This finding is further proof that Neanderthals from Mediterranean evergreen environments exploited a variety of food items, including plant materials.

The EHS from the Mediterranean evergreen (MEHS) represent a distinct group, showing similarities with the MEN, Neanderthals from steppe and coniferous forest environments and Australian aborigines, but differing from other modern hunter-gatherers (both meat-eaters and mixed-diet) and from EHS from cold environments. The occlusal wear pattern is characterized by well developed buccal phase I facets, a strong decrease of the lingual phase I facets, and prominent phase II facets. Although phase II areas are more prominent in the meat-eaters group within the modern human sample, the pronounced phase II areas have also been found in other fossil groups (such as the MEN) which clearly differ from the meat-eater modern hunter-gatherers. This result suggests that the presence of large phase II areas could be related to the exploitation of different food sources, including plant foods. The exploitation of meat was also important, as highlighted by the strong development of the buccal phase I facets (adapted to shear tough and fibrous food items), and by the similarity with the Australian aborigines, especially evident for the specimens Qafzeh 6 and 27.

The results obtained are in accordance with the buccal microwear analysis (Lalueza et al., 1996), where the Qafzeh specimens show a similar wear pattern to those of the mixed-diet modern hunter-gatherers. El Zaatari (2007), in analyzing the microwear pattern of Skhul 7 (Israel), also suggested the exploitation of a broad dietary spectrum for the Middle Paleolithic EHS from the Levantine territory; although, unlike our results, she also found similarities with the Neanderthals from deciduous forest environments. In addition, new findings from the Qafzeh Cave support the hypothesis that these hominids relied on different food sources. Numerous shells were found, indicating the exploitation of marine food as well (Bar-Yosef Mayer et al., 2009).

The Neanderthals from the steppe and coniferous forest environments (SCN) show occlusal wear patterns similar to those of the meat-eater hunter-gatherers and Australian aborigines, and different to those of the Bushmen. The SCN are characterized by large buccal phase I facets and small lingual phase I facets. As discussed above, such an example of occlusal wear is related to a high consumption of tough and fibrous food. Since these Neanderthals inhabited environments where edible plant food was scarce, the occlusal wear pattern found indicates the consumption of large quantities of animal proteins. Within the SCN sample, the specimens Vindija V259 and Monsempron 3 show an occlusal wear pattern most similar to those of the meat-eater hunter-gatherers, whereas the specimen Le Moustier 1 and Monsempron 2 show an occlusal wear pattern with elements from both meat-eater and mixed-diet hunter-gatherers. Stable isotopic signatures obtained from the analysis of the bone collagen of the Vindija specimens (Richards et al., 2000) indicate a diet mostly constituted by animal proteins. The analysis of the dental microwear of the Neanderthals from Vindija has led to similar results, showing a wear pattern similar to those of the meat-eater modern hunter-gatherers (El Zaatari, 2007).

Although El Zaatari (2007) found differences in the microwear pattern of the Neanderthals who inhabited the steppe from those that inhabited the coniferous forest environments and argued that the open environments support a low diversity of plant foods, the occlusal wear patternresults did not show any significant differences between these two types of environments. In fact, the coniferous forest biomes from the northern latitudes are also characterized by a low diversity of plant foods, due to the high acidity and low concentration of nutrients in the soil. Therefore, it is likely that the Neanderthals from the open cold environments and from the coniferous forests have exploited similar food sources, constituted mainly by animal proteins, where the intake of plant food was negligible. Pérez-Pérez et al. (2003) argued that the Neanderthals from cold Oxygen Isotope Stages (OIS) had a more abrasive diet than those from the warm OIS, due to the exploitation of plant materials such as roots and tubers. However, as previously discussed, the habitat deterioration caused by the cold temperatures provided less plant food sources than those present in the warmer environments. It is therefore unlikely that Neanderthals enduring the cold OIS had a broader dietary spectrum than those from the warm OIS.

The Upper Paleolithic *Homo sapiens* who inhabited the cold environments (SEHS) are characterized by a wear pattern similar to those of the Neanderthals of similar environments – meat-eaters and mixed-diet modern hunter-gatherers in equal measure. The buccal phase I facets are well developed whereas the lingual phase I facets are reduced. This type of pattern can probably be associated with a high consumption of meat, although other food sources may have been exploited, as suggested by the similarity with the Bushmen and Australian aborigines. The wear patterns of the Barma Grande specimens show many similarities with the Australian aborigines. These similarities could be related to the exploitation of a broader dietary spectrum; however, this was mainly constituted by animal proteins. Although the Barma Grande specimens inhabited a cold open environment, their close proximity to the sea may have created favorable conditions for plant growth, which could have provided further food sources. In addition, the numerous marine shellfish which compose the faunal assemblage found at Riparo Mochi (Barma Grande) indicate the exploitation of marine food (Stiner, 1999), confirming the hypothesis of a broader dietary spectrum for these EHS. Mladeč 2 shows an occlusal wear pattern which is strongly related to those of the meat-eater hunter-gatherers. The occlusal wear pattern of Pataud 224 is placed between those of the Australian aborigines and those of the meat-eater groups, while Sungir 2 is closer related to the meat-eaters group, sharing some similarities with the Bushmen also.

The analysis of the faunal assemblages and stone tool technology (Stiner, 1994; Svoboda et al., 2000; Bosinski, 2000; Hahn, 2000; Pérles, 2000; Hockett & Haws, 2005), the dental microwear studies (Lalueza et al., 1996; El Zaatari, 2007), and the stable isotopic signatures found in the collagen bones (Richards et al., 2001), all suggest that the Upper Paleolithic *Homo sapiens* (UPHS) consumed a wide variety of food sources. However, the occlusal wear pattern found in the UPHS does not show a great variability, suggesting a primary consumption of animal proteins, and only a secondary intake of plant materials in the specimens who inhabited the Mediterranean coastlines (with the exception of Sungir 2). These results are in accordance with the severe climatic conditions of the last glaciation, which determined the creation of environments characterized by a low diversity of plant foods.

6.4.3 Food preparation, cultural habits and paramasticatory activities

The comparison of the facet inclination, ORI and dip directions between fossil specimens who inhabited different types of environments and modern human samples have not shown any distinguishing features. However, both EHS and Neanderthals show steeper facets and higher ORI than those of the modern hunter-gatherer sample. It is probably for this reason that the EHS and Neanderthals do not show any difference in occlusal movements. In fact, the presence of a complex occlusal morphology, characterized by steep wear facets and high ORI limits the possible occlusal movements. Thus, the jaw movements of Neanderthals and EHS look to be less dependent on the type of food ingested and more dependent on the occlusal morphology. In contrast, the flatter occlusal surfaces of the modern hunter-gatherer sample permit wider and more diversified masticatory movements, which are less constrained from the occlusal morphology and more dependant on the physical properties of the ingested food. In fact, as discussed above, the analysis of the dip directions (especially of the LRT and LPT wear facets) allow us to distinguish between modern hunter-gatherers who relied on a diet mostly based on animal proteins, from those who consumed a mixed-diet.

The flat occlusal surface of the modern hunter-gatherers may be related to the consumption of a more abrasive diet. However, within the modern human sample, groups such as the Inuit, Fuegians and Vancouver Islanders (who mostly consumed foods low in abrasiveness like meat and fish), show an occlusal wear characterized by flatter surfaces than those of the Bushmen, who consumed highly abrasive food items. This is due to the fact that the abrasiveness of the diet does not depend solely on the physical properties of the food itself but also by the exogenous materials contained in the food (e.g. Luke & Lucas, 1983; Kaifu et al., 2003; Kaidonis, 2008). Therefore, the amount of abrasive materials introduced into the mouth also depends on the type of food preparation and eating habits (e.g. Molnar, 1972).

In the Inuit populations, meat and/or fish was frequently kept frozen underground and eaten raw, or dried on open racks (Leigh, 1928; Sinclair, 1952; Giddings, 1967; De Poncins 1978). The Vancouver Islanders used to store large quantities of salmon in drying and smoking houses (Ames & Maschner, 1999). Australian aborigines used to cook their food in improvised ovens by digging pits in the earth (Begg, 1954; O'Dea, 1991). These food preparation methods introduced a large quantity of exogenous materials, such as sand, dust or ashes. In addition, meat desiccation determines a change of its physical properties, causing an increase in toughness (Molnar, 1972). In fact, as noted by Taylor (1963):

> "*Dried shark meat provided "bush" rations for the Maori when they traveled, and the meat was a food that required a tremendous amount of hard chewing in order to reduce it to the point that the bolus could be swallowed*"

Therefore, it is likely that the flat occlusal surfaces (low ORI and low wear-facet inclinations) found in the hunter-gatherer groups are related to the food preparation method, which causes the increased intake of highly abrasive foreign particles together with changes to the physical properties of the food.

These results are similar to those obtained by El Zaatari (2007, 2008a), where the meat-eater hunter-gatherers from the northern latitudes (such as Tigara, Alaska), show a higher level of dental surface complexity than those of the Khoe-San (Bushmen). Although the Khoe-San inhabited a desert environment, they did not dry their meat nor cook it in earth ovens (El Zaatari 2007, 2008a).

As suggested by this author, the complexity (and therefore the flatness) of the occlusal surfaces of the Bushmen dentition, is mainly due to the intrinsic level of abrasiveness of the ingested food items, such as seeds, roots or tubers, rather than dust or sand included incidentally in the diet.

The Australian aborigines exhibit the flattest dental occlusal surface within the entire modern hunter-gatherer group. In this case, the flat occlusal surface is the result of the combination of the incidental introduction of exogenous materials (through food preparation) into the mouth, and the abrasive properties of the plant materials ingested. Unlike the microwear studies (El

Zaatari, 2007, 2008a), which showed a low tooth surface complexity indicating the intake of a low-abrasive diet, the occlusal wear pattern of the Fuegians analyzed here displays low wear facet inclination and low ORI, suggesting the consumption of a highly abrasive diet. Although, as highlighted by El Zaatari (2007, 2008a), little information about food preparation in the Fuegian tribes is available from ethnographic or historic data; it cannot be assumed that Fuegians did not have food preparation methods which increased the abrasiveness of their diet.

The presence of complex occlusal tooth surfaces in the Neanderthal and EHS samples, characterized by steep wear facets and high ORI, suggests the use of simple and unsophisticated food preparation methods, which resulted in the intake of a low-abrasive diet. El Zaatari (2007) found similar results, highlighting in particular that no Neanderthals have shown a level of surface complexity comparable to those of modern hunter-gatherers from Point Hope, Alaska and the Andaman Islands.

Cooking, together with food preparation, changes the physical properties of foods very radically (Lucas, 2004). Cooking reduces physical barriers, changes molecular structure, reduces toxin loads and defrosts (Stahl, 1984; Brace, 1995; Wrangham & Conklin-Brittain, 2003). It also reduces the toughness, tenderizing meat and softening plant foods (Wrangham, 2007).

The use and control of fire dates back to the Middle Paleolithic to at least 250,000 years ago and probably as early as 300,000-500,000 years ago (James, 1989; Straus, 1989; Gamble, 1993; Monnier et al., 1994; Brace, 1995; Wrangham, 2007). It is reasonable to think therefore, that both the Neanderthals and EHS included in our sample were able to use fire for cooking, since the control of fire is much older than the specimens considered here. All modern hunter-gatherers cook their food. However, evidence exists for the consumption of raw meat in the human populations with a hunter-gatherer subsistence. As discussed previously, for instance, the Inuit, , frequently eat raw meat (Leigh, 1928; Sinclair, 1952; Giddings, 1967; De Poncins 1978). Raw meat requires a long chewing time before it can be reduced to smaller pieces and swallowed (Wrangham & Conklin-Brittain, 2003; Duncan & Lieberman, 2008). The toughness of meat depends on the proportion of collagen and connective tissue (Bender, 1982; Dransfield, 1994; Purslow, 1999; Lucas and Peters, 2000; Wrangham & Conklin-Brittain, 2003). Prolonged mastication of raw meat would probably increase the degree of wear. From the analysis of the occlusal wear pattern in modern hunter-gatherers, it was not possible to distinguish specimens who relied on the intake of a large quantity of raw meat, such as the Inuit, from populations who frequently cooked their meat. However, it can be argued that the steep wear facets and high ORI which characterize the occlusal surfaces of the maxillary molars of EHS and Neanderthals, could suggest a consumption of cooked meat, or the intake of raw meat with low toughness, such as the organs and other parts of the animal having a low proportion of collagen and connective tissue.

Paramasticatory activities should also be given consideration. As discussed above, the upper molars of the modern hunter-gatherers, and in particular the molars of the Inuit, Vancouver Islanders and Fuegians, are frequently (27% of the entire modern hunter-gatherers sample) characterized by enamel splintering on the buccal side (dental chipping), indicating the crushing of hard objects such as bones (Turner II & Cadien, 1969). Other non-dietary habits are mentioned in the ethnographic literature, such as the repeated mastication of tough pieces of skin, or the use of teeth as tools for holding and/or carrying objects, tearing and cutting animal meat and clothing (Buxton, 1920; Leigh, 1925; Pederson, 1938, 1949; Mitchell, 1959; Gould, 1968; Balikci, 1970; Molnar, 1972).

In Neanderthals, the advanced degree of wear of the frontal teeth, with large dentine exposures and rounded labial wear (Brace, 1967), has been interpreted as evidence for the use of the anterior dentition as a third hand in processing food and other materials (Molnar, 1972; Lumley, 1973; Trinkaus, 1983; Frayer and Russel, 1987; Bermudez de Castro et al., 1988; Lalueza Fox and Frayer, 1997). However, the absence of "particulars" types of tooth wear in the postcanine dentition in the Neanderthal and EHS sample (such as the dental chipping in the maxillary molars) suggests that the posterior dentition of the modern hunter-gatherers underwent greater stress than that exerted on the fossil sample. These types of stress probably caused (in concomitance with the different food preparation methods) an increase of the flatness of the occlusal dental surface.

6.5 Food competition between Neanderthals and early *Homo sapiens*

Neanderthals and early *Homo sapiens* (EHS) who inhabited the European continent during Oxygen Isotope Stage (OIS) 3 show a similar occlusal wear pattern, indicating a diet low in diversity, consisting mostly of animal proteins.

The analysis of stable isotopes (e.g. Fizet et al., 1995; Bocherens et al., 1999, 2001, 2005; Richards et al., 2000, 2001; Pettitt et al., 2003; Drucker & Bocherens, 2004; Beauval et al., 2006), faunal assemblages (e.g. Stiner, 1994; Svoboda et al., 2000; Bosinski, 2000; Hahn, 2000; Patou-Matis, 2000; Pérles, 2000; Aura Tortosa et al., 2002; Burke, 2004), and dental microwear

(Lalueza et al., 1996; El Zaatari, 2007), have led to hypothesize that the Neanderthals who occupied northern and central Europe during OIS 3 had a low diversified diet focused on large and medium-sized terrestrial herbivores, while the european Upper Paleolithic *Homo sapiens* (UPHS) relied on a broader dietary spectrum including small, non-mammalian animals and plant foods. In particular, Hockett & Haws (2005) argued that the consumption of a low diversified diet would have led to an impoverishment of essential nutrients, an increase in maternal and non-fetus-to-infant mortality and a decreased average life expectancy. Subsequently, the exploitation of a more diversified diet including both high-energetic food sources (such as animal proteins) and micronutrient-rich plant foods, may have positively affected the demographic expansions of the EHS populations, leading to the replacement of the Neanderthals in Europe during OIS 3 (Hockett & Haws, 2005).

If Neanderthals and the EHS from OIS 3 relied on the exploitation of different food sources, the variations in diet should be reflected through the differing use of teeth and the resulting wear patterns. Despite the small sample size (Neanderthals, N=4; EHS, N=5) and the absence of the latest Neanderthals (Saint-Césaire 1, Zafarraya or Vindija V-207 and V-208), the analysis of the occlusal wear pattern in Neanderthals and the EHS who inhabited Europe during OIS 3 did not show any significant difference. The occlusal wear pattern in Neanderthals indicates a diet mostly based on animal proteins, as suggested by previous studies. Likewise, the reduced variability in the wear pattern, and the strong similarity with the Neanderthals, suggest that EHS had a restricted dietary spectrum, where the diet was dominated by the intake of animal proteins.

These results support the hypothesis that during the last glaciations Neanderthals and EHS competed for the same food resources. The habitat deterioration caused an impoverishment of the food diversity, especially reducing the availability and variety of plant foods in northern and central Europe. In the southern latitudes, less severe climatic conditions favoured the formation of habitats which provided a more diversified diet, including plant materials, small animals and marine food sources along the coastlines. In fact, the close similarity in the occlusal wear between Australian aborigines and the Barma Grande specimens can be explained by the exploitation of a slightly broader dietary spectrum, as also indicated by the numerous marine shellfish found at Riparo Mochi (Stiner, 1999). However, the Neanderthals who lived in southern Europe were also able to exploit other food sources (apart from the meat from large and medium-sized herbivores). The presence of marine animals (seals, dolphins, tortoises, fish and molluscs) and small terrestrial animals (lagomorphs, insectivores, rodents and molluscs), in the Mousterian cave deposits along the Mediterranean coastlines of

Italy and Gibraltar (Stiner, 1994; Barton, 2000; Finlayson et al., 2006; Stringer et al., 2008), indicate the exploitation of similar resources to those at Barma Grande. It is important to note that no Neanderthals that inhabited southern Europe during OIS 3 have been included in the analysis. Nevertheless, Amud 1, a Neanderthal specimen who lived in the Levantine territory around 55,000 years ago, shows an occlusal wear pattern different from those of Neanderthals who occupied central Europe during OIS 3, suggesting the exploitation of different food sources, including plant materials.

The analysis of the occlusal wear pattern and new evidence from the mediterranean Mousterian caves, suggests that Neanderthals and EHS would probably have competed for the same food sources (animal proteins from large and medium-sized herbivores in central and northern Europe; plant materials, medium and small vertebrates including marine foods in southern Europe). The lack of essential nutrients due to the exploitation of similar food sources in central and northern Europe, would not only have affected the Neanderthals negatively, but also the EHS population. Therefore, from the analysis of occlusal wear, the hypothesis that a more diversified diet favoured the EHS over the Neanderthals as suggested by Hockett & Haws (2005) seems unconvincing.

The more advanced technology used by the EHS compared to that of Neanderthals, has been considered one of the possible causes leading to the expansion of the EHS through Europe at the expense of the Neanderthals (e.g. Mellars, 2004; Banks et al., 2008). In particular, the discovery of grinding stone tools in the Dolní Věstonice site, suggests the exploitation of plant materials by the UPHS (Svoboda et al., 2000). However, food preparation techniques (such as grinding) which introduced grit into the food, increased the abrasiveness of the diet (e.g. Molnar, 1972). Therefore, if the EHS developed sophisticated food processing methods, as seen in the modern hunter-gatherer populations, they should show an occlusal wear pattern typical of an abrasive diet. However, the analysis of the wear facet inclination and the occlusal relief index, did not display any differences between Neanderthals and EHS; on the contrary they exhibit an occlusal surface characterized by steeper wear facets and higher ORI than those of the modern hunter-gatherers. These results indicate that both Neanderthals and the EHS had a less abrasive diet than those of modern hunter-gatherers, mostly due to the absence of sophisticated food processing methods in the Pleistocene hominids.

Although, a more advanced technology would have certainly favoured the EHS in hunting and exploiting freshwater food sources (Richards et al., 2001), the occlusal wear pattern does not show any sign of better food processing methods than those used by Neanderthals.

Several causes probably influenced the demographic decline of the Neanderthal populations during the last glaciations. The severe and fluctuating climatic conditions and reduced availability and variability of food sources, combined with the arrival of EHS in Europe (equipped with a more advanced stone tool technology and characterized by a complex social organization), would probably have intensified the competition for the already scarce resources, leading Neanderthals to extinction.

Chapter 7

Conclusion

Neanderthals inhabited western Eurasia from about 200,000 BP to 30,000 BP, occupying different geographical areas and facing the severe climatic fluctuations which characterized the Pleistocene epoch. The majority of studies, based mostly on the analysis of faunal remains (e.g. Patou-Matis, 2000) and stable isotopic signatures (e.g. Fizet et al., 1995; Bocherens et al., 1999; Richards et al., 2000; Drucker & Bocherens, 2004; Beauval et al., 2006), have led to the hypothesis that Neanderthals were active hunters fed mostly on animal proteins from large and medium-sized herbivores. The same studies (e.g. Patou-Matis, 2000; Richards et al., 2001; Pettitt et al., 2003; Burke, 2004), including dental microwear analysis (Lalueza et al., 1996; El Zaatari, 2007), have suggested that early *Homo sapiens* (EHS) had a broader dietary spectrum, including the consumption of plant foods and small mammalian and non-mammalian animals. The arrival of EHS in Europe during the cold Oxygen Isotope Stage 3, equipped with a more advanced tool technology and a complex social organization, created an intensified competition with the Neanderthal populations for the already scarce resources due to the habitat deterioration which characterized the last glaciations (e.g. Stringer et al., 2003; Mellars, 2004; Banks et al., 2008). In addition, the intake of more diversified essential nutrients probably favored a demographic expansion of the EHS populations, leading to the replacement of Neanderthals in Europe (Hockett & Haws, 2005).

However, the methods applied for the reconstruction of the Neanderthal's diet have some limitations. The archaeological records are mostly composed of faunal remains, since bones preserve better than plant materials. Consequently, the analysis of faunal remains tends to overestimate the consumption of meat and underestimate the consumption of plant food, giving the impression that diet was mostly consisted of animal proteins (Mann, 1981; Hastorf, 1988). Stable isotope analyses are destructive methods which require good bone collagen preservation, limiting the Neanderthal sample which can be analyzed. Moreover, as animal sources have higher protein fractions than those of plant foods, the isotopic studies of bone collagen are overrepresented by animal proteins at the expense of the vegetable proteins (Sponheimer & Thorp, 2007). New evidences coming from the archaeological records of Neanderthal sites in southern Europe (Stiner, 1994; Barton, 2000; Finlayson et al., 2006; Stringer et al., 2008) and Near East (Albert et al., 2000; Madella et al., 2002; Lev et al., 2005; Henry & Piperno, 2008), indicate that Neanderthals exploited different food sources, including the intake of plant materials and marine foods, contradicting the results obtained from the faunal remains and stable isotope analyses.

Occlusal wear pattern, unlike the dental microwear which is affected by the "The Last Supper" phenomenon (Grine, 1981) due to rapid pattern changes in relation to diet, is a cumulative process occurring during the lifespan of the individual, and thus reflects the diet over a long term (Janis, 1990).

In the present study, we have analyzed the occlusal wear pattern of maxillary molars of Neanderthals and EHS who occupied different geographical areas at different chronological times, using a non-destructive method based on three-dimensional polygonal models generated from surface scanning of dental casts. In order to evaluate how dietary differences influence the occlusal wear pattern, upper molars of modern hunter-gatherers with known diet and different dietary habits have been included in the sample and compared with those of Neanderthals and EHS.

The occlusal wear pattern of the carnivorous hunter-gatherers (Inuit, Vancouver Islanders and Fuegians) differs from those of mixed-diet hunter-gatherers (Australian aborigines and Bushmen). In particular, the study of the relative areas better distinguishes meat-eaters from mixed-diet hunter-gatherers, while the occlusal relief index (ORI) and the wear facet inclinations seem to be more related to the abrasiveness of the diet, mostly due to the introduction of exogenous materials during food preparation. The strong development of the buccal phase I facets (as seen in the meat-eaters hunter-gatherers) is associated with the processing division of tough and fibrous food such as meat, whereas the presence of large lingual phase I facets (as seen in the mixed-diet hunter-gatherers) is related to an omnivore diet, where a greater transverse component of the jaw movements is necessary for the processing of plant materials. The phase II wear facets, instead, result to be less distinctive, showing no significant differences between meat-eaters and mixed-diet hunter-gatherers. The analysis of the dip directions has shown a significant difference in the lateroretrusive (LRT) and lateroprotrusive (LPT) facets between meat-eaters and mixed-diet hunter-gatherers, while the study of the mediotrusive (MT) and medioprotrusive (MPT) facets highlighted a large variability, causing a marked overlap between the specimens belonging to the two different dietary groups. The high variability characterizing phase II movements (MT and MPT) is mostly related to the dip direction of facet 10 and facet 11, which instead of pointing towards MT and MPT respectively, are directed in the opposing directions (MPT and MT respectively).

The Neanderthal occlusal wear pattern is characterized by an ecogeographic variation and it is possible to distinguish three main groups inhabiting three different environments: deciduous woodland, Mediterannean evergreen and steppe/coniferous forest. The Neanderthals from deciduous woodlands (DWN) display an occlusal wear pattern characterized by a reduction of the buccal phase I facets and an increase of the lingual phase I facets, differing significantly from the meat-eaters modern hunter-gatherers. This type of wear pattern, associated with a large variability, suggests the exploitation of different food sources including plant foods. The Mediterranean Neanderthals (MEN) exhibit an occlusal wear pattern similar to those of DWN, while the Neanderthals from steppe/coniferous forest environments (SCN) show an occlusal wear pattern characterized by a reduced variability and a strong similarity to meat-eaters modern hunter-gatherers (marked buccal phase I facets and reduced lingual phase I facets), indicating a restricted dietary spectrum based mostly on the intake of animal proteins.

EHS sample has been divided into two groups: those who inhabited the Mediterannean environments (MEHS) and those who lived in the steppe/coniferous forest habitats (SEHS). The MEHS show a wear pattern characterized by well developed buccal phase I facets and large phase II facets, indicating the exploitation of animal and plant foods, as also suggested by the similarity to MEN. The faunal remains analysis, stable isotope and dental microwear studies suggest the exploitation of broader dietary spectrum in Upper Paleolithic *Homo sapiens*. To the contrary the occlusal wear pattern of SEHS shows strong similarities to those of SCN and meat-eaters hunter-gatherers, indicating a diet mostly constituted by animal proteins.

The development of the wear facets along the slopes of the four main cusps in the first and second upper molars reflect in part the results obtained by Bailey (2002a), indicating a relationship between tooth morphology and tooth wear. However, the variability exhibited within the Neanderthals, EHS and MHG group, and the similarity between specimens belonging to different taxonomic groups inhabiting similar environments, suggests that the occlusal wear pattern of the fossil hominids considered in this study is strongly related to the type of environment, and consequently dependent on the exploitation of different food sources.

The analysis of wear facet inclination and ORI in Neanderthals and EHS does not show any differentiation between the two Pleistocene hominids, and between the fossil specimens inhabiting different environments. However, if the fossil group is compared to the MHG sample, a significant difference is found. Both Neanderthals and EHS are characterized by steep wear facets and high ORI values, whereas MHG show a flat occlusal surface. As mentioned previously, the use of different food preparation methods by the modern hunter-gatherers, such as desiccation, smoking or frozening, causes the intake of exogenous materials like dust, ash or sand with the ingested food, increasing the abrasiveness of their diet. The complex occlusal relief of Neanderthals and EHS and the resulting occlusal tooth wear, could be explained by the consumption of a low abrasive diet, which is probably due to the use of simple and unsophisticated food preparation techniques.

Moreover, the common presence of enamel splintering (dental chipping) in the maxillary molars of the MHG (especially marked in the Inuit, Vancouver Islanders and Fuegians), and its complete absence in the Neanderthals and EHS examined here, suggests a differentiation in dietary habits and paramasticatory activities between the modern and the fossil sample.

In conclusion, the similar occlusal wear pattern (relative wear areas, dip angle and occlusal relief index) between Neanderthals and EHS who inhabited Europe during the cold OIS 3, suggests the use of similar and simple food preparation methods and the exploitation of similar and low-diversified food sources, indicating an intense competition between the two Pleistocene hominids.

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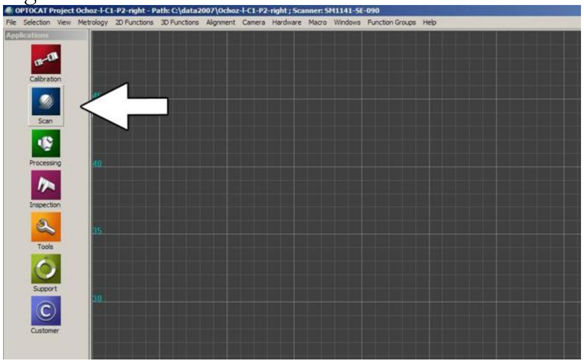
Appendix A

In this Appendix the steps necessary for generating 3D polygonal models from surface scanning are illustrated. In particular the Appendix is focused on the collection and alignment of the scan-data carried out through the software optoCAT 2007 (Breuckmann, GmbH).

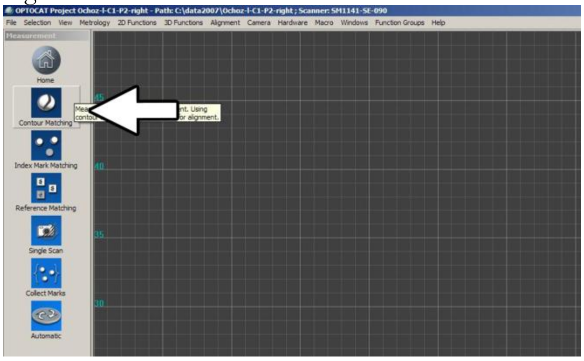
Step 1. Setting the parameters prior surface scanning

Figure B1.



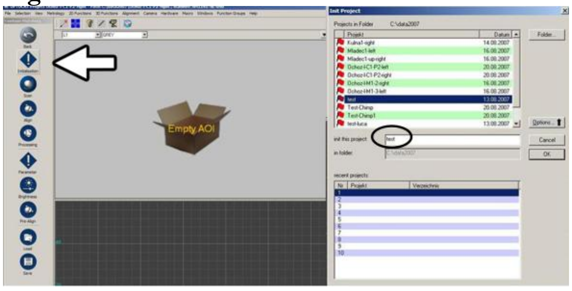
- Once that the software is open you have to click on the icon Scan that you find on the left side (figure A1).

Figure A2.



- Click on Contour Matching (figure A2).

Figure A3



Projects in Folder C:\data2007

Projekt	Datum
Kulna1-right	14.08.2007
Mladec1-left	16.08.2007
Mladec1-up-right	16.08.2007
Ochoz-I-C1-P2-left	20.08.2007
Ochoz-I-C1-P2-right	20.08.2007
Ochoz-I-M1-2-right	16.08.2007
Ochoz-I-M1-3-left	16.08.2007
test	13.08.2007
Test-Chimp	20.08.2007
Test-Chimp1	20.08.2007
test-luca	13.08.2007

init this project: test

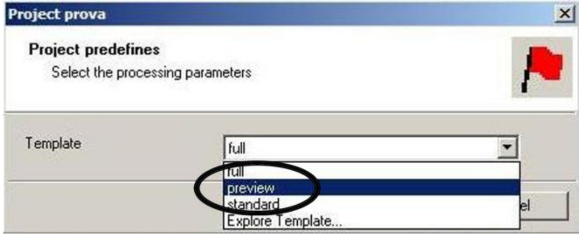
in folder: C:\data2007

recent projects:

Nr	Projekt	Verzeichnis
1		
2		
3		
4		
5		
6		
7		
8		
9		
10		

- Click on Initialization, and then type the new project name selecting the preferred folder (figure A3).

Figure A4.



Project prova

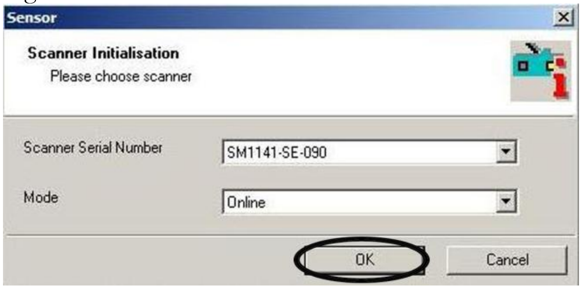
Project predefines

Select the processing parameters

Template: full

- In the Project predefines window select the preview template (figureA4).

Figure A5.



Sensor

Scanner Initialisation

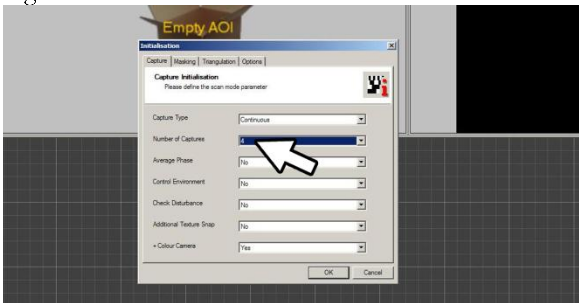
Please choose scanner

Scanner Serial Number: SM1141-SE-090

Mode: Online

- In the Scanner Initialisation window, leave the default setting and click on OK (figure A5).

Figure A6.



Capture Initialisation

Please define the scan mode parameter

Capture Type: Continuous

Number of Captures: 4

Average Phase: No

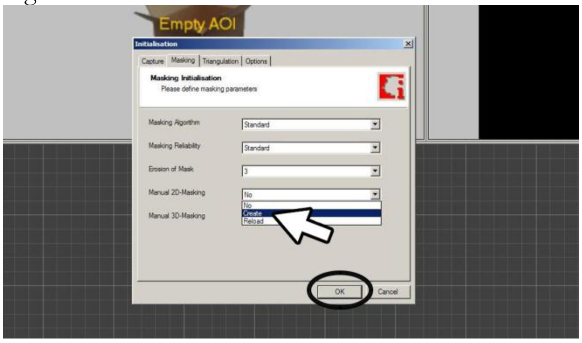
Control Environment: No

Check Disturbance: No

Additional Texture Snap: No

+ Colour Camera: Yes

Figure A7.



Masking Initialisation

Please define masking parameters

Masking Algorithm: Standard

Masking Reliability: Standard

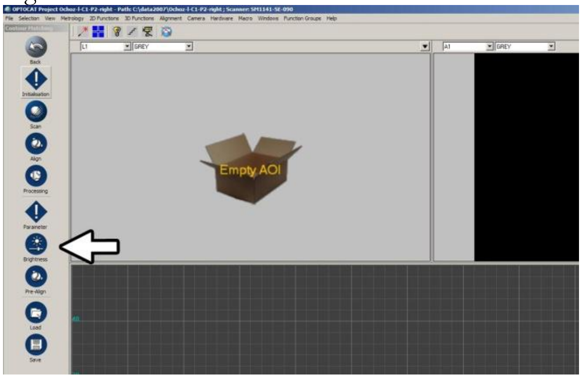
Erosion of Mask: 3

Manual 2D-Masking: No

Manual 3D-Masking

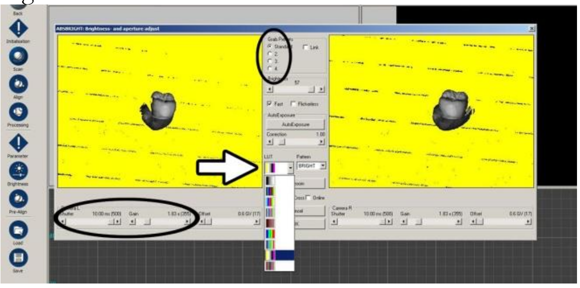
- In the Parameter setting, click on the Capture menu (top of the window) and select 4 as Number of Captures (figure A6). Afterwards click on the Masking Menu (top of the window) and select Manual 2D-Masking then Create option. Subsequently click on OK (figure A7).

Figure A8.



- Click on the Brightness icon situated on the left side of the screen (figure A8).

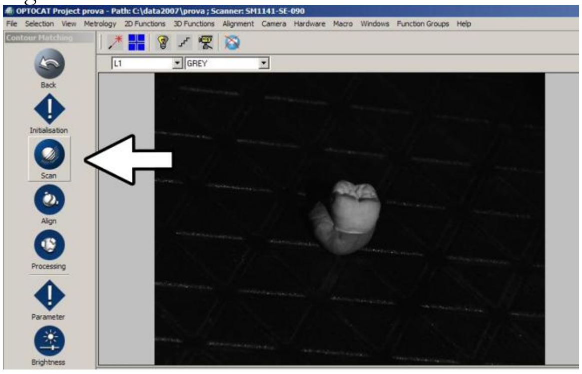
Figure A9.



- In the middle of the screen click on LUT and select the light pattern as highlighted in figure A9. Afterwards set each grab preset (top of the screen) adjusting shutter and gain values (on the bottom left).

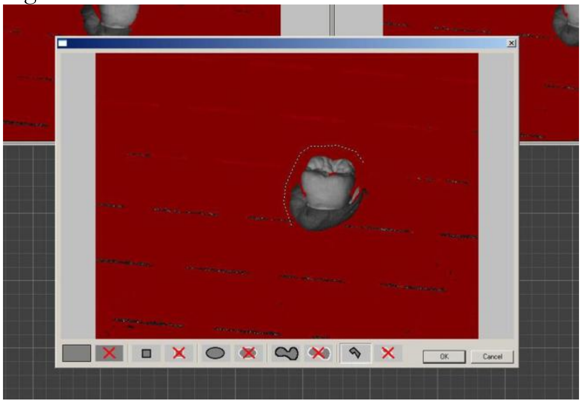
Step 2. Collection and alignment of the scan-data

Figure A10.



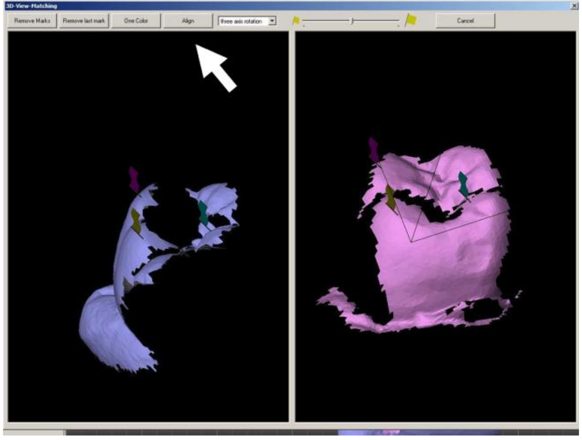
- Click on the Scan icon to start the object scanning (figure A10).

Figure A11.



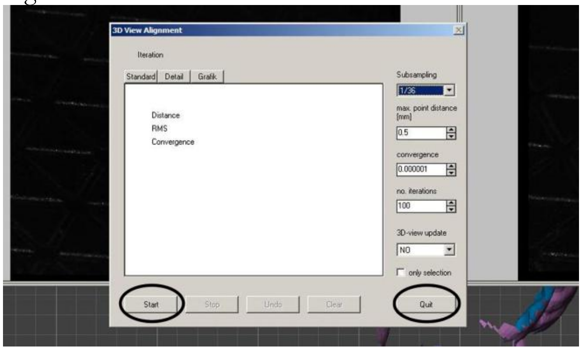
- Once the surface scanner has finished taking the image, a new window will appear where it is possible to crop the image just captured (figure A11).

Figure A12.



- In order to align the different views captured it is necessary to select three homologous landmarks on each of the two images, and then click on the Align button (figure A12). To select the landmarks press the Ctrl key and click the left mouse button.

Figure A13.



Subsampling: 1/36

max. point distance [mm]: 0.5

convergence: 0.000001

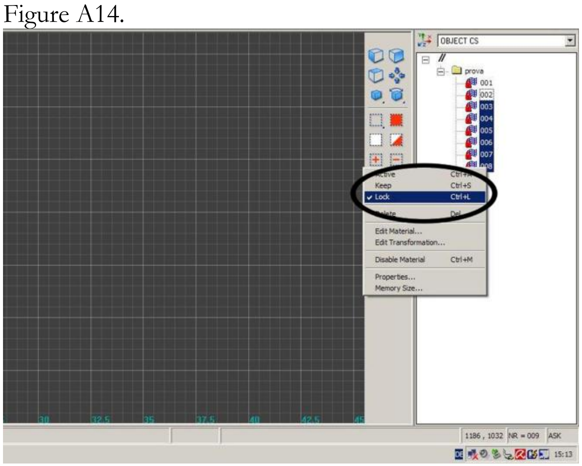
no. iterations: 100

3D-view update: NO

☐ only selection

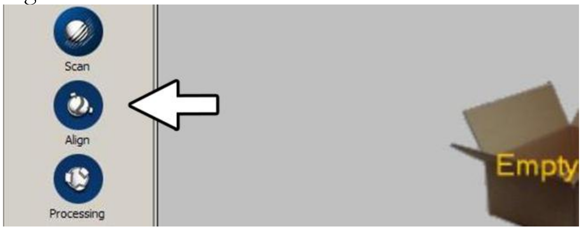
- Once the manual alignment is concluded, a small window will appear: click on Start and then Quit (figure A13).

Figure A14.



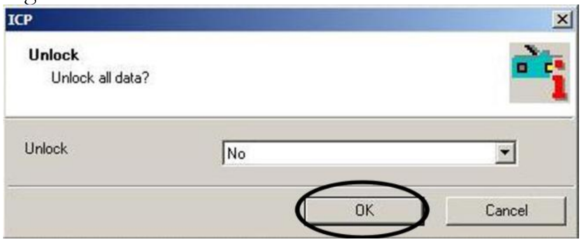
- Once a complete scanning of the object is obtained, the images captured have to be locked with the exception of the first view. Select all the images (from the second to the last one) and click the right mouse button to lock them (figure A14).

Figure A15.



- Back to the left menu and click on Align (figure A15).

Figure A16.


ICP

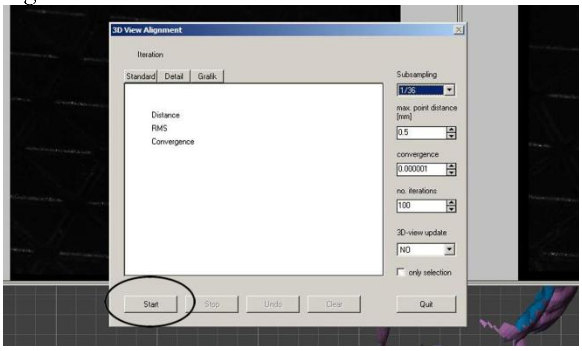
Unlock

Unlock all data?

Unlock: No

- After the alignment a small window will ask if you want to unlock all the data. Leave the default setting and click on OK (figure A16).

Figure A17.


3D View Alignment

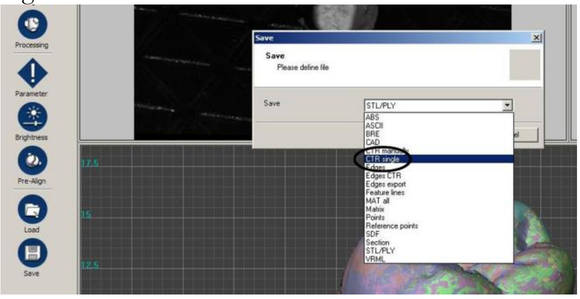
Iteration

Distance
RMS
Convergence

Subsampling: 1/36
max. point distance [mm]: 0.5
convergence: 0.000001
no. iterations: 100
3D-view update: NO
☐ only selection

- On the 3D View Alignment window, the images have to be subsampled starting from1/36 to 1/1. For each Subsampling click on Start and then Quit (figure A17).

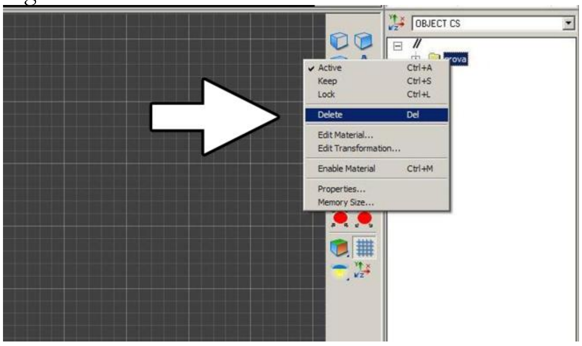
Figure A18.



- On the left menu click on Save, selecting the CTR single extension and click on OK (figure A18).

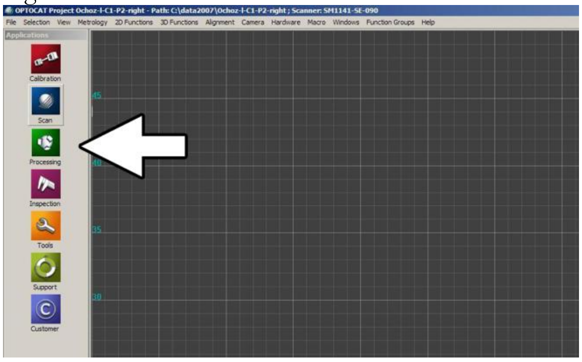
Sep 3. 3D Data Processing

Figure A19.



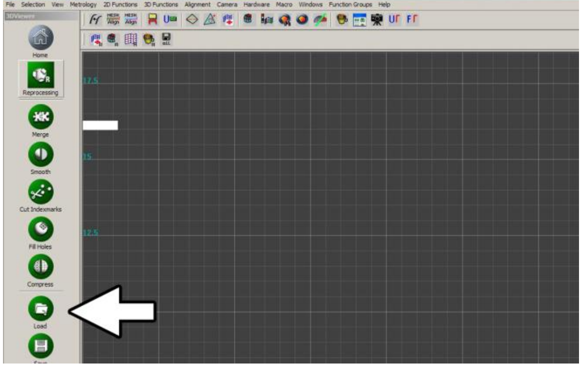
- On the Object window manually delete the folder just created (figure A19). Afterwards, on the menu on the left click Back and then Home.

Figure A20.



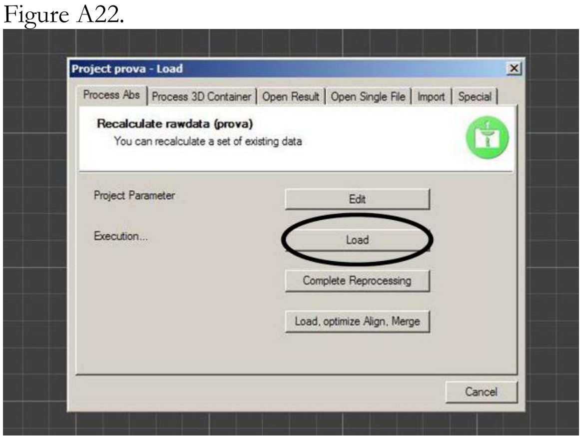
- To start the postprocessing of the object click on the Processing icon on the left (figure A20).

Figure A21.



- Once you have entered the Processing window click on Load (figure A21).

Figure A22.


Project prova - Load

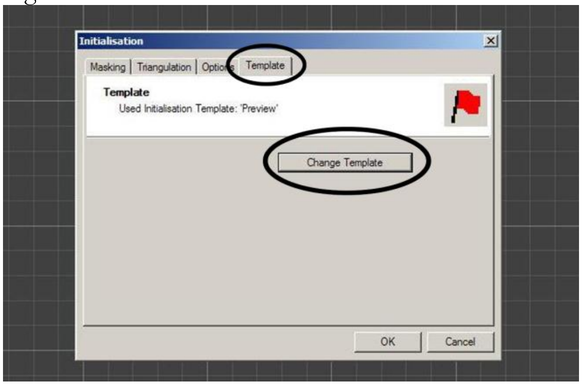
Recalculate rawdata (prova)
You can recalculate a set of existing data

Project Parameter

Execution...

- In the Project Parameter window click on load (figure A22).

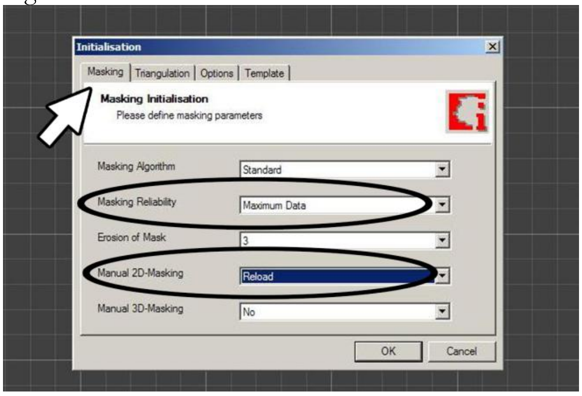
Figure A23.


Initialisation

Template
Used Initialisation Template: 'Preview'

- In the Initialisation window, select Template (on top of the screen) and click on Change Template (figure A23).

Figure A24.

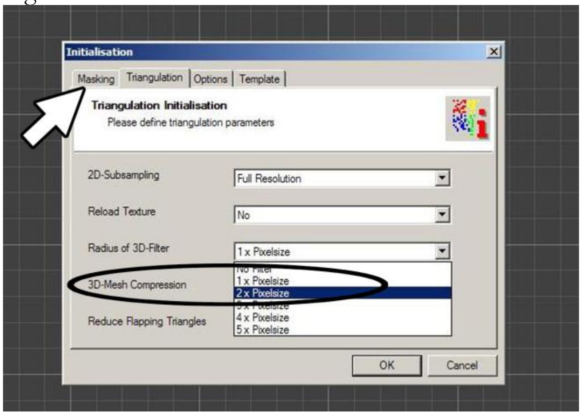

Initialisation

Masking Initialisation
Please define masking parameters

Masking Algorithm: Standard
Masking Reliability: Maximum Data
Erosion of Mask: 3
Manual 2D-Masking: Reload
Manual 3D-Masking: No

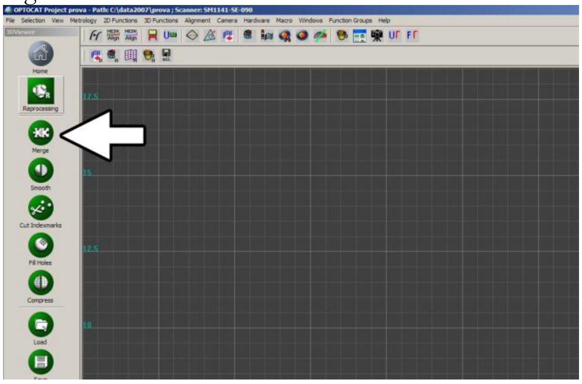
- In the Initialisation window always click on Masking (on top of the screen). In Masking Reliability select Maximum Data, while in Manual 2D-Masking select Reload (figure A24).

Figure A25.



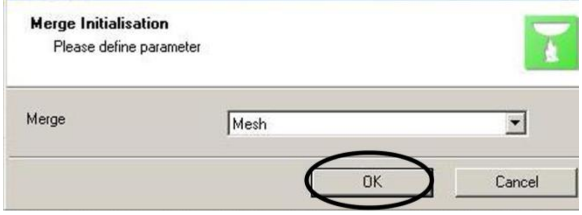
- In the Initialisation window, click on Triangulation and select 2x Pixelsize for Radius of 3D-Filter (figure A25).

Figure A26.



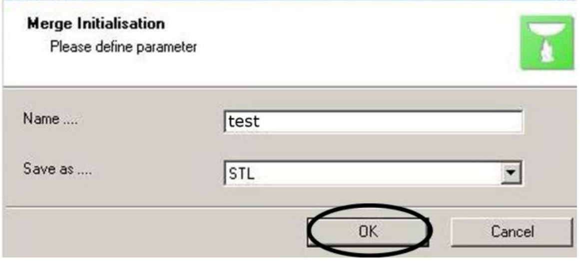
- Once the Processing is finished, click on Back and then click on Merge (figure A26).

Figure A27.



- In the Merge Initialisation window leave the default setting and click on OK (figure A27).

Figure A28.



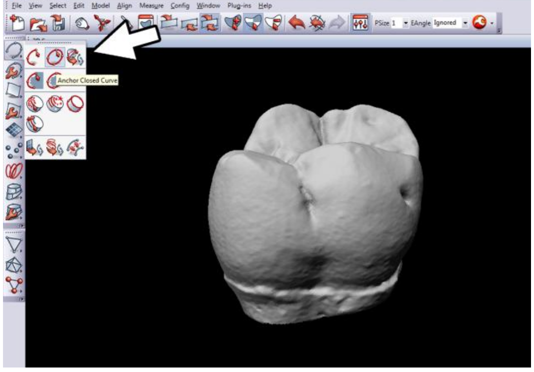
- Name the file and save as STL file format (figure A28).

Appendix B

The Occlusal Fingerprint Analysis method (OFA) is explained in detail in this appendix. The measurements on the 3D digital model were obtained using the IMEdit and IMInspect modules of Polyworks® Version 10.0 (InnovMetric Software Inc.). The appendix is divided into four sections: Orientation, Surface Area, 3D Occlusal Compass and Occlusal Relief Index (ORI).

1. Orientation

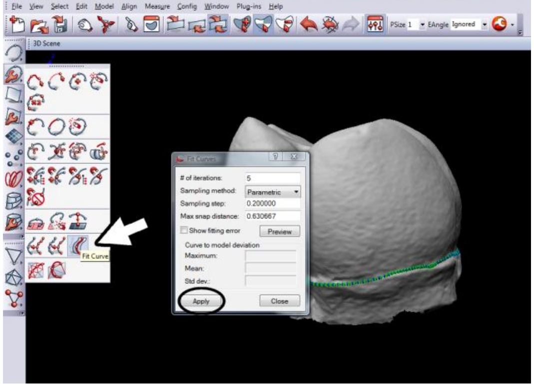
Figure B1.1.



- Select the IMEdit module of Polyworks® and import the polygonal model.

- The first step is to insert a polyline in correspondence to the cervical line. In Curve Creation (left menu) click on Anchor Closed Curve, and insert the polyline (figure B1.1).

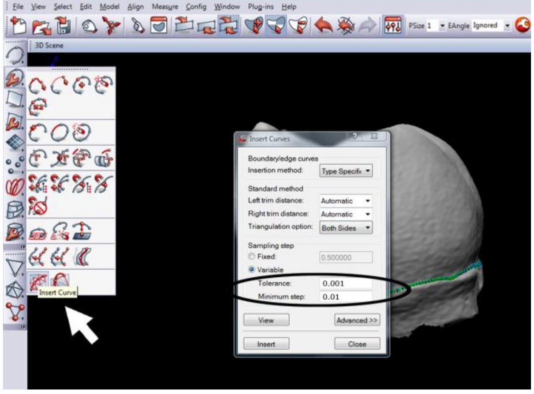
Figure B1.2.



# of iterations: 5
Sampling method: Parametric
Sampling step: 0.200000
Max snap distance: 0.630667
☐ Show fitting error

- Select the Curve Editor and click on Fit Curve, leaving the default setting in the following window, clicking on Apply (figure B1.2).

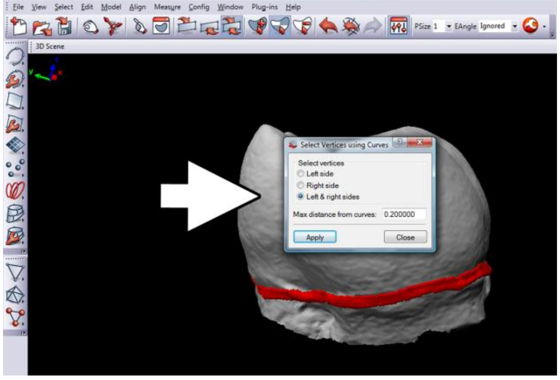
Figure B1.3.



Boundary/edge curves
Insertion method: Type Specific
Standard method
Left trim distance: Automatic
Right trim distance: Automatic
Triangulation option: Both Sides
Sampling step
○ Fixed: 0.500000
● Variable
Tolerance: 0.001
Minimum step: 0.01

- Afterwards (always in the Editor Curve) click on Insert Curve and in the following window set the Tolerance to 0.001 and the Minimum step to 0.01 (figure B1.3).

Figure B1.4.



Select Vertices using Curves

Select vertices

○ Left side

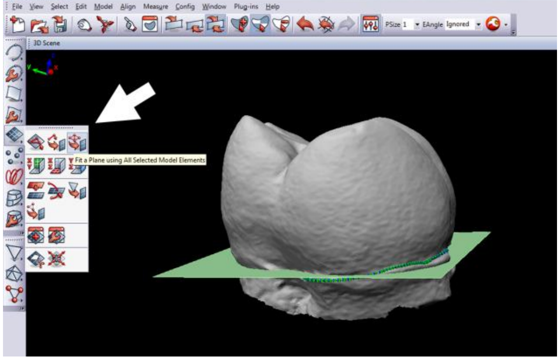
○ Right side

● Left & right sides

Max distance from curves: 0.200000

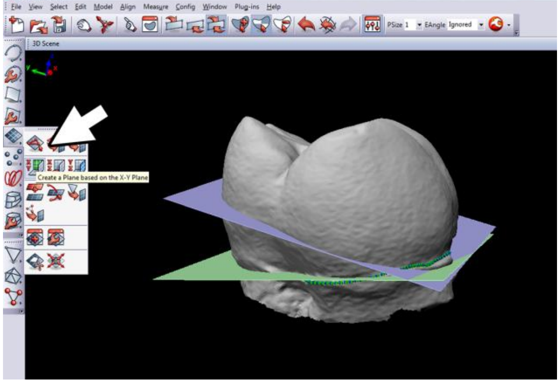
- On the top menu, click on Select-> Vertices-> and Left & Right Sides of Curves. On the following window select Left & right sides and set the Max distance from curves value to 0.2 (figure B1.4).

Figure B1.5.



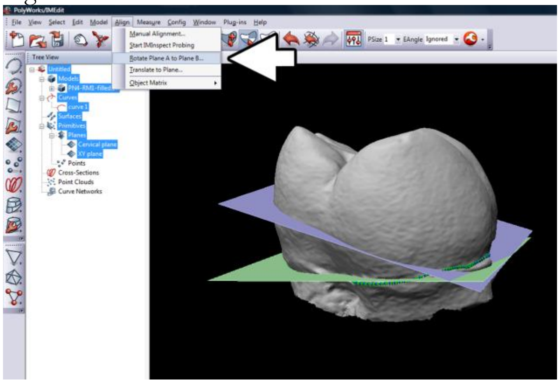
- On the left menu select Plane creation and editing and click on Fit a plane using all selected model elements (figure B1.5).

Figure B1.6.



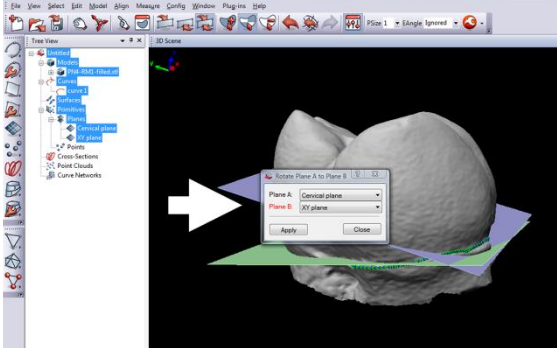
- Create a Plane based on the X-Y plane clicking on the corresponding icon in the Plane creation and editing menu (figure B1.6).

Figure B1.7.



- Manually select all the objects created in the Tree View menu, and click on Align (top menu) selecting Rotate Plane A to Plane B (figure B1.7).

Figure B1.8.

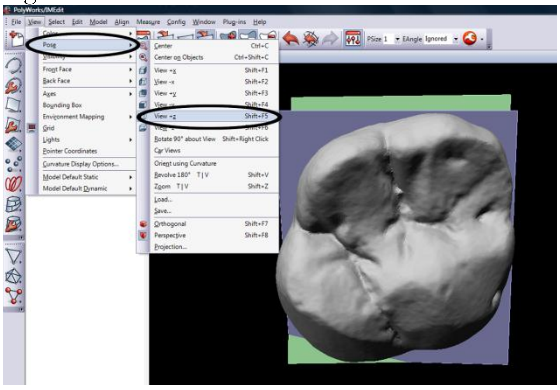


Plane A: Cervical plane

Plane B: XY plane

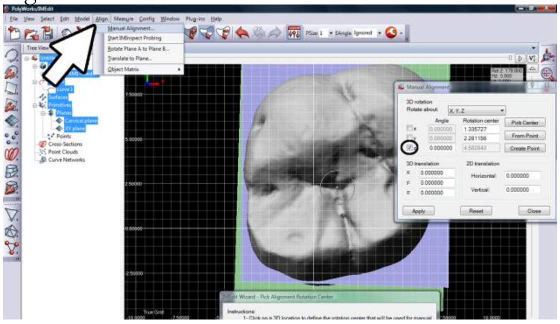
- Set the Cervical plane as Plane A and set the XY plane as Plane B, and then click on Apply (figure B1.8).

Figure B1.9.



- In the View menu (top of the screen) select Pose and then View +z (figure B1.9).

Figure B1.10.



3D rotation

Rotate about: X, Y, Z

	Angle	Rotation center
☐ x	0.000000	1.335727
☐ y	0.000000	2.281156
☑ z	0.000000	4.502842

3D translation

x: 0.000000

y: 0.000000

z: 0.000000

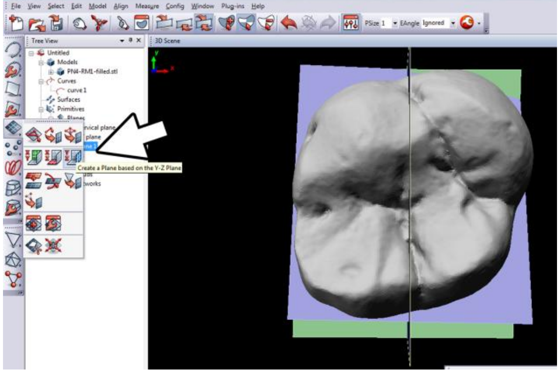
2D translation

Horizontal: 0.000000

Vertical: 0.000000

- Click on Align (top menu) and select Manual Alignment. In the following window select Pick Center, positioning the circle in correspondence to the central fossa. Afterwards check the box of the z axis, manually aligning the mesial (or distal) side of the tooth crown in correspondence to the vertical axis of the grid and click on Apply (figure B1.10).

Figure B1.11

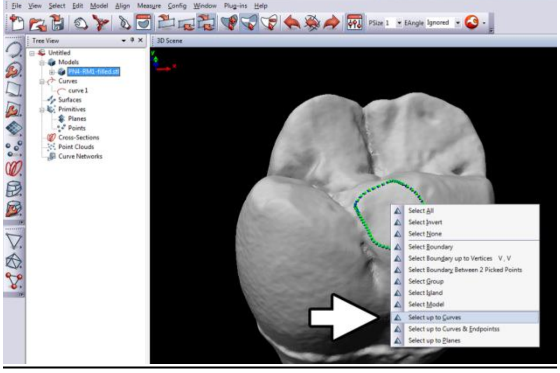


- Once the tooth orientation is complete, create an YZ plane from the (figure B1.11).

2. Surface Area

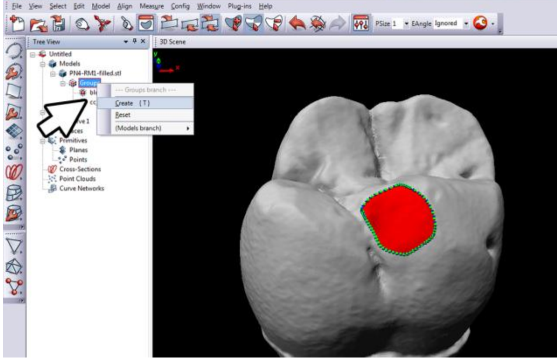
- Each facet has to be manually outlined inserting a polyline on the digital polygonal model. Therefore the same steps seen previously with creation of the Cervical line must be repeated.

Figure B2.1.



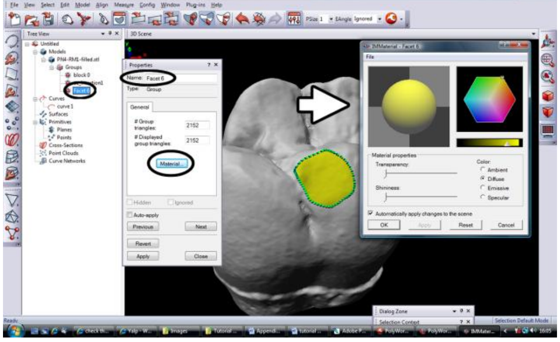
- Once the facet is outlined, press the Space bar and click on the polygonal model in correspondence to the facet with the right mouse button and, holding the Shift key at the same time. In the following window click on Select up to Curves (figure B2.1).

Figure B2.2.



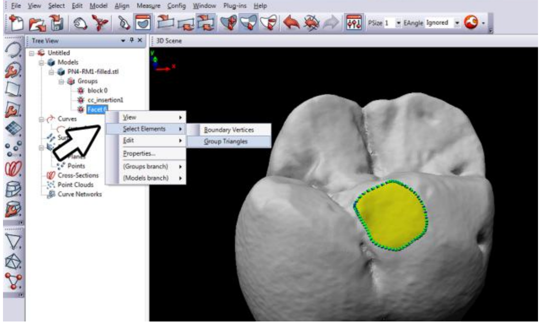
- In the Tree View menu, click on the polygonal model file and afterwards click on the Groups icon with the right mouse button, selecting Create (figure B2.2).

Figure B2.3.



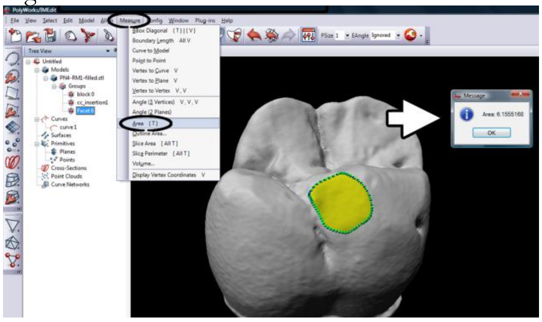
- Rename the Groups file just created (default1), and click on Apply. Select Material and change the facet color; then click on OK (figure B2.3).

Figure B2.4.



- Select the facet icon in the Groups branch with the right mouse button. Click on Select Elements and afterwards on Group Triangles (figure B2.4).

Figure B2.5.

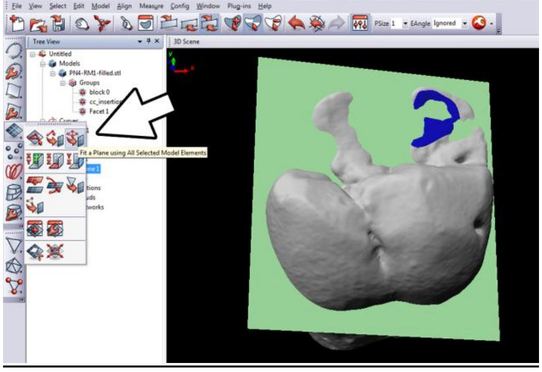


Area: 6.1555168

- On the top menu select Measure and click on Area. A small window will appear showing the value of the area in mm^2 (figure B2.5).

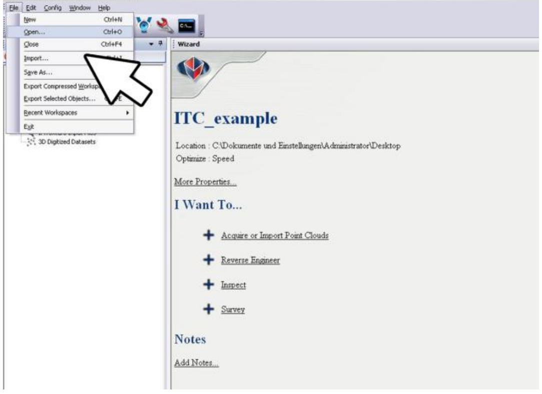
3. 3D Occlusal Compass

Figure B3.1



- Select the group triangles of the facet as seen above, and click on Fit a Plane Using All Selected Model Elements in the Plane creation and editing menu (figure B3.1). Save the file and close the IMEdit module.

Figure B3.2.



ITC_example

Location : C:\Dokumente und Einstellungen\Administrator\Desktop
Optimize : Speed

More Properties...

I Want To...

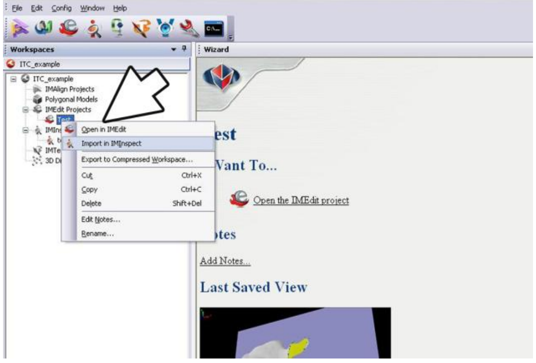
+ Acquire or Import Point Clouds
+ Reverse Engineer
+ Inspect
+ Survey

Notes

Add Notes...

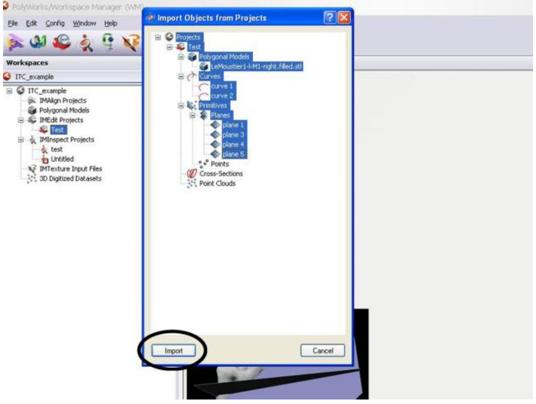
- In the Workspace Manager click on File->Open selecting the project just created (figure B3.2).

Figure B3.3.



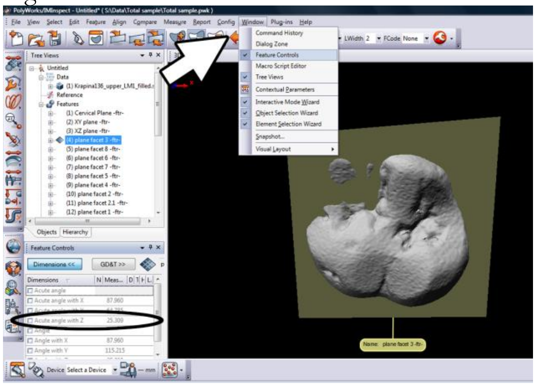
- Select the project and click on the right mouse button. In the following window select Import in IMInspect (figure B3.5).

Figure B3.4.



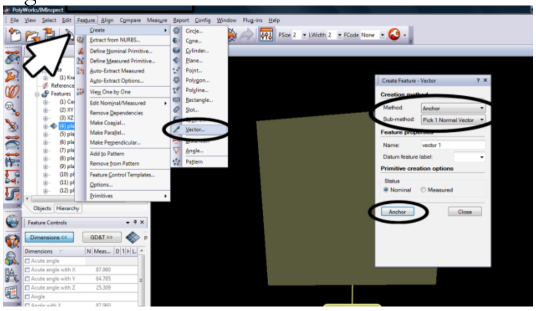
- In the following window select all the objects you want to import in IMInspect (figure B3.4).

Figure B3.5.



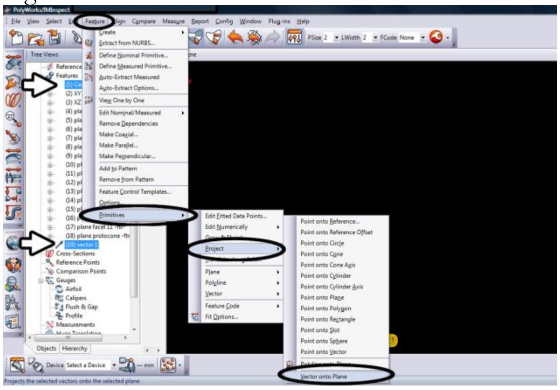
- In order to calculate the dip angle of each facet click on Window (top menu) and select Feature Controls. Select the facet plane in the Tree Views menu, and on the bottom (Feature Controls menu) the dip angle is displayed as an Acute angle with z (figure B3.5).

Figure B3.6.



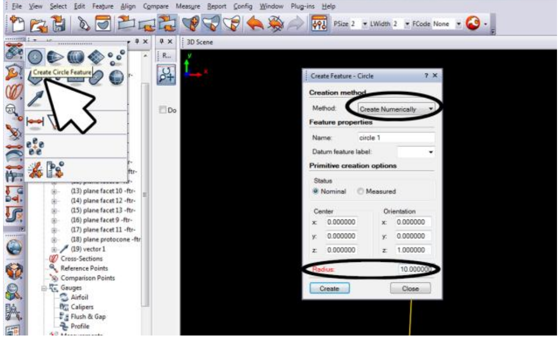
- Select the facet plane (Tree Views menu) and click on Feature (top menu). Afterwards select Create and click on Vector. In the following window select Anchor in Method, and Pick 1 Normal Vector in Sub-Method. Finally click on Anchor and pick a landmark on the surface of the plane (figure B3.6).

Figure B3.7.



- Concurrently select (holding the Ctrl key) the vector just created and the cervical plane. On the top menu click on Feature selecting Primitive->Project and Vector onto Plane (figure B3.7).

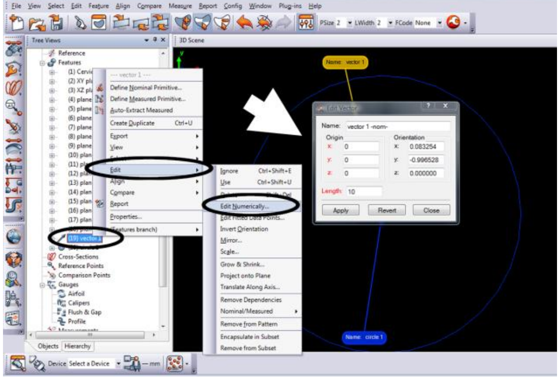
Figure B3.8.



Method: Create Numerically
Name: circle 1
Center x: 0.000000 y: 0.000000 z: 0.000000
Orientation x: 0.000000 y: 0.000000 z: 1.000000
Radius: 10.000000

- On the left menu click on Feature Creation and select Create Circle Feature. In the following window select Create Numerically in Method, and leave the default settings with the exception of the Radius changing the value to 10.0 (figure B3.8).

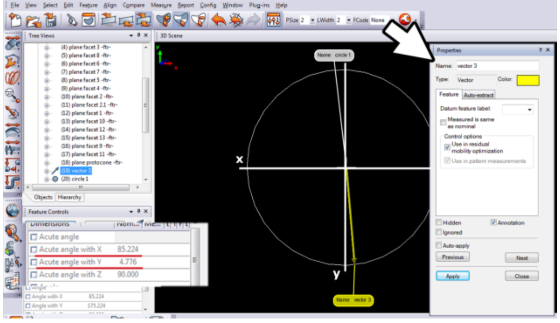
Figure B3.9.



Name: vector 1 -nom-
Origin x: 0 y: 0 z: 0
Orientation x: 0.083254 y: -0.996528 z: 0.000000
Length: 10

- Select the Vector in the Tree Views menu, and click on the right mouse button. In the following window select Edit->Edit Numerically and set the Origin values to 0 and the Length to 10. Finally click on Apply (figure B3.9).

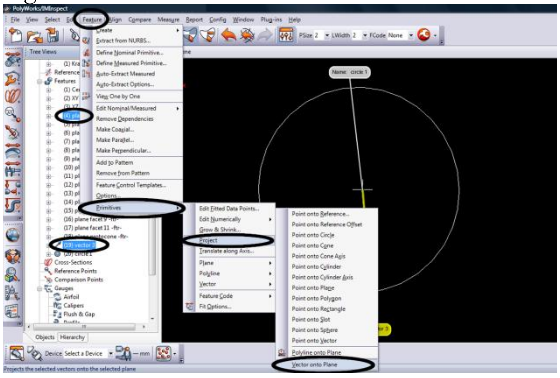
Figure B3.10



Name: vector 3
Acute angle with X 85.224
Acute angle with Y 4.776
Acute angle with Z 90.000
Angle with X 85.224
Angle with Y 175.224

- The Vector properties (name and color) can be changed double clicking on the Vector (Tree Views Menu). In order to calculate the dip direction of each facet, the intersection between the vector and X or Y axis is added or subtracted to 90°. The angles are displayed in the Feature Controls menu as Acute angles with X and Y (figure B3.10).

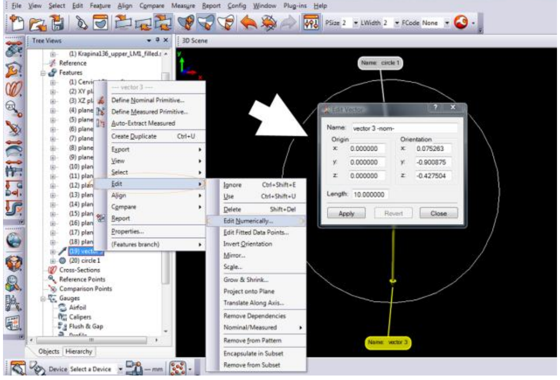
Figure B3.11.



Projects the selected vectors onto the selected plane

- In order to create the 3D Occlusal compass, each vector has to be projected on its plane. Select the vector and its corresponding plane, click on Features (top menu), selecting Primitive, then Projects and lastly Vector onto Plane (figure B3.11).

Figure B3.12.



Name: vector 3 -nom-

Origin
x: 0.000000
y: 0.000000
z: 0.000000

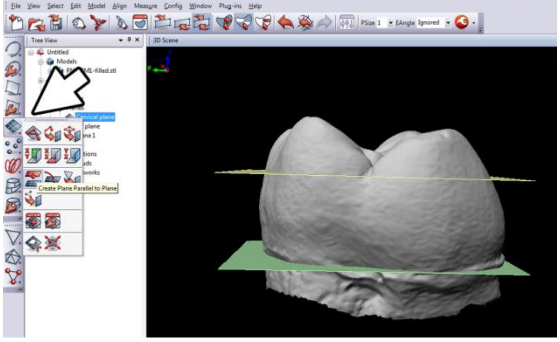
Orientation
x: 0.075263
y: -0.900875
z: -0.427504

Length: 10.000000

- Click on the Vector (right mouse button), and on the following menu select Edit, then Edit Numerically, setting the values of the XYZ axes (Origin) to 0 and the Length to 10.0 (figure B3.12).

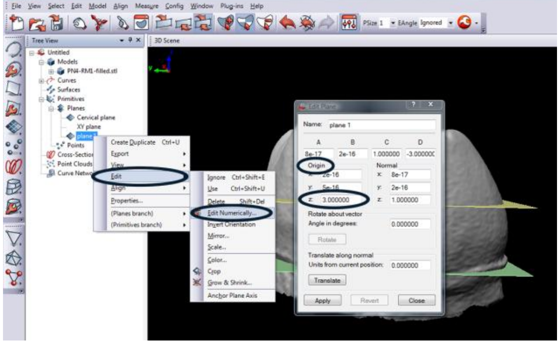
4. Occlusal Relief Index

Figure B4.1.



- Open IMEdit module selecting the project file (including the polygonal model already orientated with the cervical plane) and in Plane Creation and Editing click on Create Plane Parallel to Plane (figure B4.1).

Figure B4.2.



Name: plane 1

A	B	C	D
8e-17	2e-16	1.000000	-3.00000C

Origin
x: 2e-16
y: 5e-16
z: 3.000000

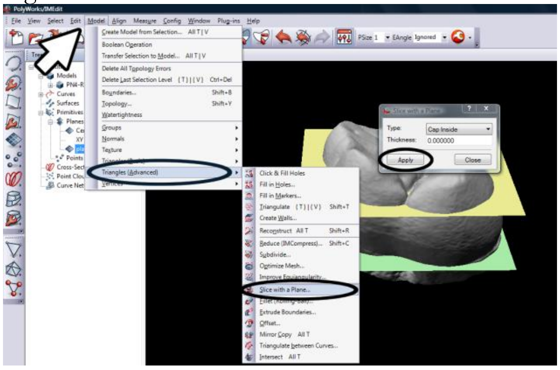
Normal
x: 8e-17
y: 2e-16
z: 1.000000

Rotate about vector
Angle in degrees: 0.000000

Translate along normal
Units from current position: 0.000000

- The plane just created must be adjusted in order that it coincides with the lowest occlusal point. Click with the right mouse button on the object Plane (Tree Views menu) and select Edit and Edit Numerically. In the following window set the z value (Origin) moving the Plane to the lowest occlusal point (figure B4.2).

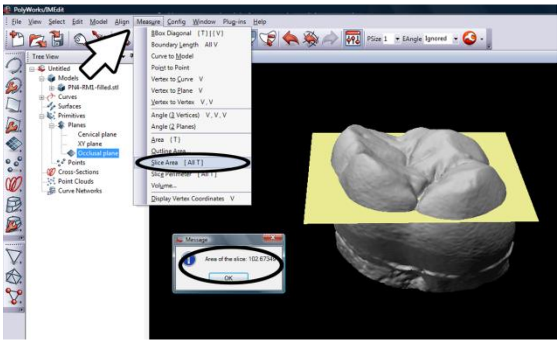
Figure B4.3.



Type: Cap Inside
Thickness: 0.000000

- Click on Model (top menu) and select Triangles (Advanced) and Slice with a Plane. In the following window leave the default settings and click on Apply (figure B4.3).

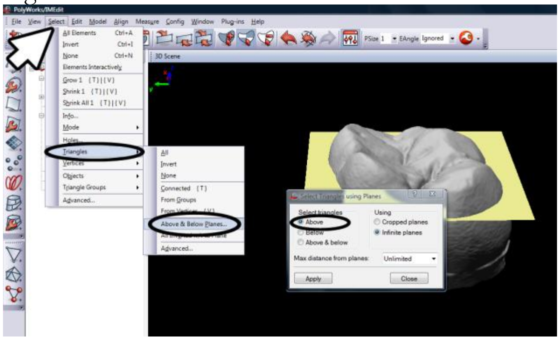
Figure B4.4



Area of the slice: 102.67349

- In order to measure the surface 2D area of the Occlusal plane click on Measure (top menu) and select Slice Area. Area value is shown in the following window (figure B4.4).

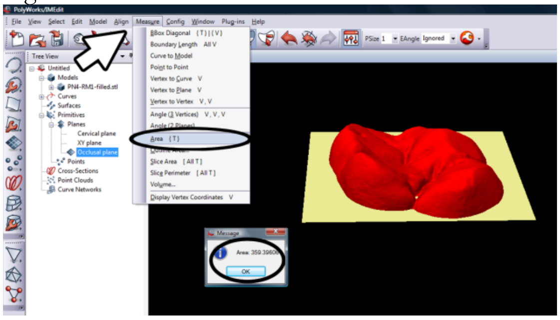
Figure B4.5.



Select triangles: ● Above ○ Below ○ Above & below
Using: ○ Cropped planes ● Infinite planes
Max distance from planes: Unlimited

- Click on Select (top menu) and select Triangles and Above & Below Planes. In the following window check Above and click on Apply (figure B4.5).

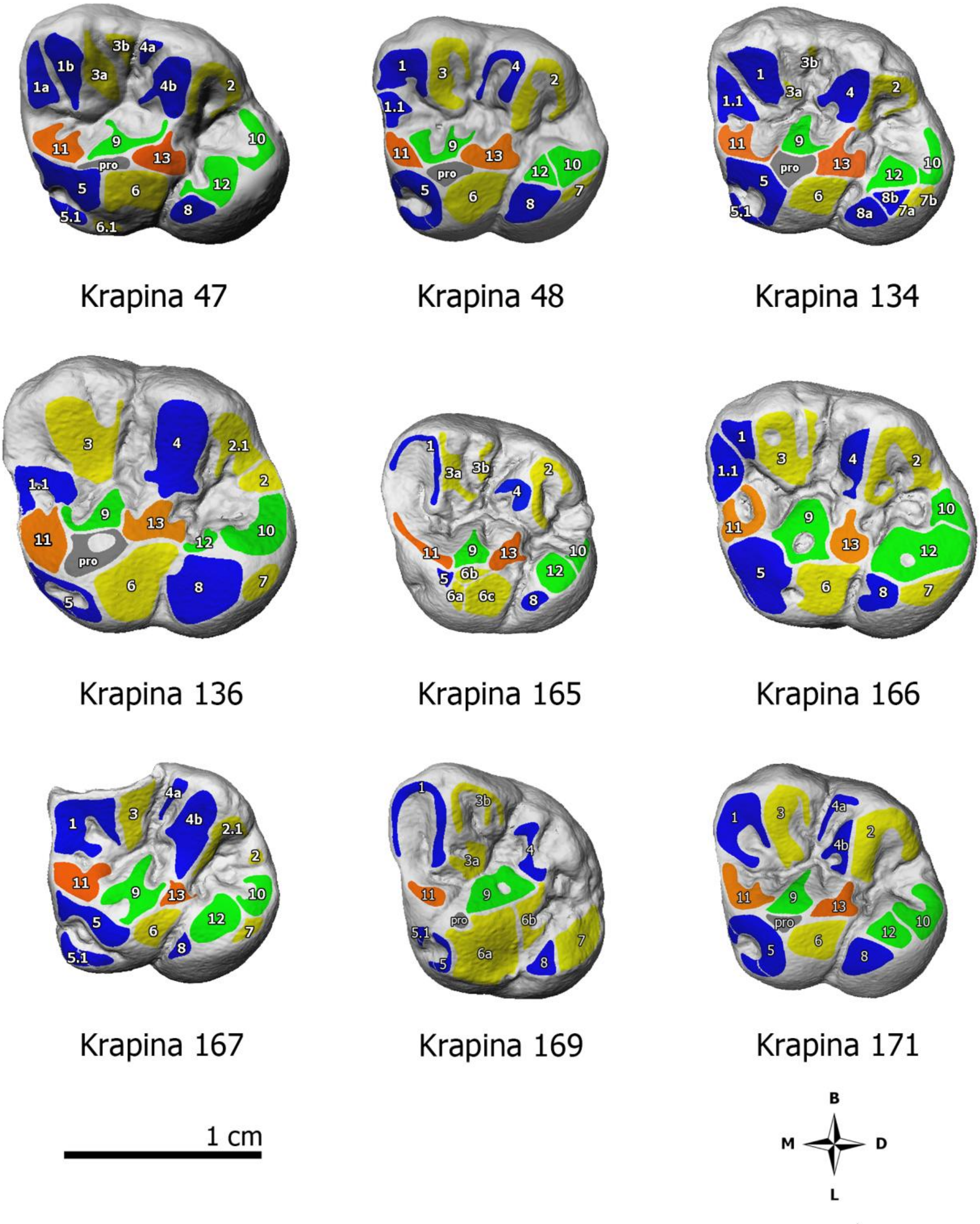
Figure B4.6.



Area: 359.39606

- Click on Measure (top menu) select Area, and the following window will give the value of the 3D Area (figure B4.6)

Appendix C



Krapina 47

Krapina 48

Krapina 134

Krapina 136

Krapina 165

Krapina 166

Krapina 167

Krapina 169

Krapina 171

Figure C1


Krapina 172

Krapina 175

Krapina 177

Tabun 1

Monsempron 2

Monsempron 3

Shanidar 2

Amud 1

Vindija V259

Figure C2

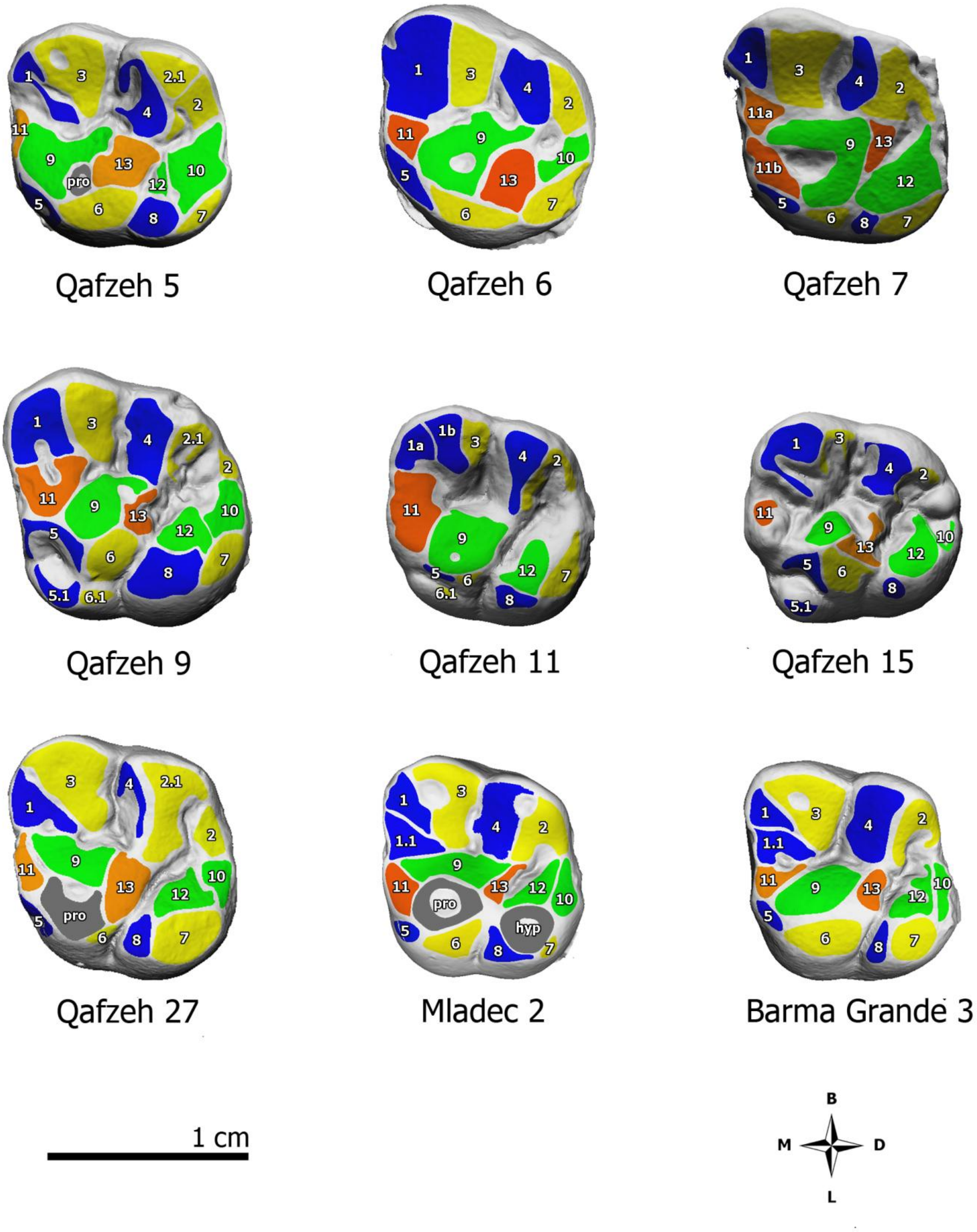

Qafzeh 5
Qafzeh 6
Qafzeh 7
Qafzeh 9
Qafzeh 11
Qafzeh 15
Qafzeh 27
Mladec 2
Barma Grande 3
1 cm
B
M
D
L
pro
hyp

Figure C3

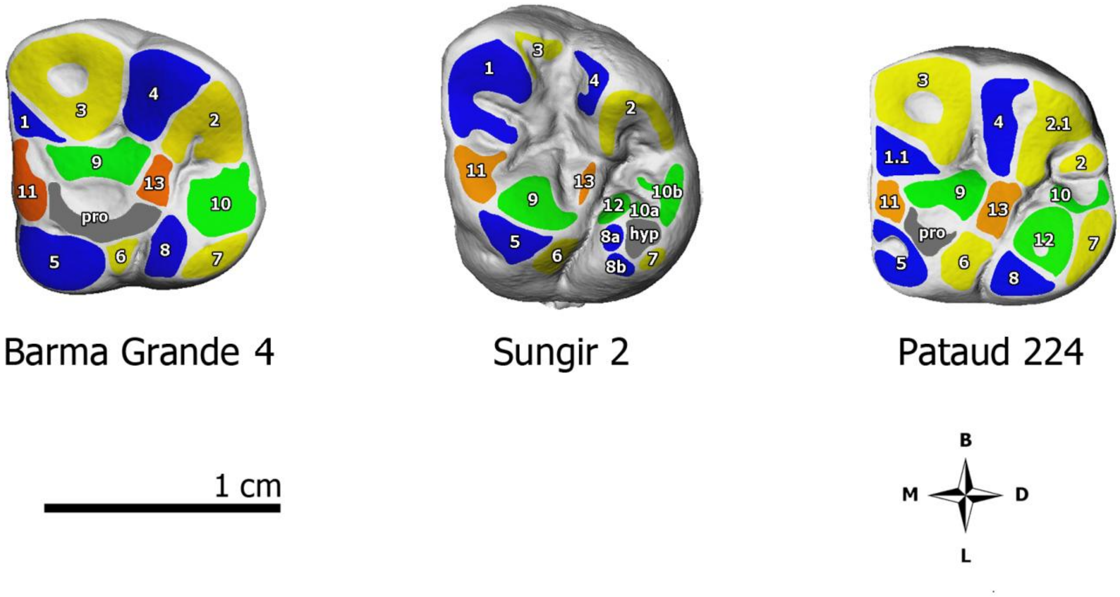


Figure C4

Occlusal wear pattern in Neanderthals (Fig. C1 and C2) and early *Homo sapiens* (Fig. C3 and C4) dentition. Polygonal digital models of teeth obtained from surface scanning (smartSCAN 3D, Breuckmann GmbH) of dental stone casts. Wear facets were manually outlined onto the digital models using the IMEdit module of Polyworks® v.10.1 (InnovMetric Software Inc.). Wear facets are color-coded following the dental occlusal concept (Kullmer et al., 2009). Orientation: buccal (B); distal (D); mesial (M); lingual (L).

Appendix D

NEA	*Wear2*	*Wear3*
Wear2	***	0.1548
Wear3	0.1548	***

EHS	*Wear2*	*Wear3*
Wear2	***	0.6144
Wear3	0.6144	***

MHG	*Wear2*	*Wear3*
Wear2	***	0.7591
Wear3	0.7591	***

Table D1. Comparison (NPMANOVA) between maxillary molars differing in degree of wear (2 and 3) within Neanderthal (NEA), early *Homo sapiens* (EHS) and the modern hunter-gatherers (MHG) group, taking into account the relative areas of buccal, lingual and phase II facets. Significant p-values (<0.05) are highlighted in red.

NEA	M^1	M^2
M^1	***	0.7183
M^2	0.7183	***

MHG	M^1	M^2
M^1	***	0.001
M^2	0.001	***

Table D2. Comparison (NPMANOVA) between M^1 and M^2 within Neanderthals (NEA) and the modern hunter-gatherers (MHG) group, taking into account the relative areas of buccal, lingual and phase II facets. Significant p-values (<0.05) are highlighted in red.

INUIT	M^1	M^2
M^1	***	0.4478
M^2	0.4478	***

VANC.	M^1	M^2
M^1	***	0.0152
M^2	0.0152	***

Table D3. Comparison (NPMANOVA) between M^1 and M^2 within the Inuit and Vancouver Islanders (Vanc.), taking into account the relative areas of buccal, lingual and phase II facets. Significant p-values (<0.05) are highlighted in red.

BUCCAL	*Wear 2*	*Wear 3*
Wear 2	***	1.30E-05
Wear 3	1.30E-05	***

LINGUAL	*Wear 2*	*Wear 3*
Wear 2	***	0.0064
Wear 3	0.0064	***

PHASE II	*Wear 2*	*Wear 3*
Wear 2	***	0.0001
Wear 3	0.0001	***

TOTAL	*Wear 2*	*Wear 3*
Wear 2	***	5.10E-07
Wear 3	5.10E-07	***

Table D4. Comparison (Mann-Whitney U-test) between wear facets (Buccal, Lingual, Phase II and Total) belonging to molars differing in degree of wear (2 and 3), taking into account the dip angle. Significant p-values (<0.05) are highlighted in red.

ORI	*Wear 2*	*Wear 3*
Wear 2	***	0.0599
Wear 3	0.0599	***

Table D5. Comparison (Mann-Whitney U-test) between maxillary molars differing in degree of wear (2 and 3), considering the occlusal relif index (ORI). Significant p-values (<0.05) are highlighted in red.

Table D6. Descriptive statistics (mean and standard deviation) of relative buccal, lingual and phase II facet areas, within the modern hunter-gatherer groups.

		Buccal		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD
Inuit	10	49.7	4.1	15.5	5.0	33.4	5.4
Vancouver Is.	15	47.3	3.4	16.9	9.5	32.6	9.5
Fuegians	7	47.1	2.0	13.9	6.3	30.7	8.5
Australians	3	46.7	1.1	21.3	4.5	30.0	6.2
Bushmen	7	45.0	4.6	27.1	5.5	24.4	4.4

Table D7. Comparison (Permutation t test) between modern hunter-gatherer groups considering the relative areas of buccal, lingual and phase II facets. Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

BUCCAL	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.1177	0.1344	0.2191	0.0461
Vancouver Is.	1	***	0.9271	0.7770	0.2084
Fuegians	1	1	***	0.7617	0.3039
Australians	1	1	1	***	0.5670
Bushmen	0.461	1	1	1	***

LINGUAL	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.6498	0.5465	0.1013	0.0012
Vancouver Is.	1	***	0.4326	0.4595	0.0171
Fuegians	1	1	***	0.1012	0.0037
Australians	1	1	1	***	0.1683
Bushmen	0.012	0.171	0.037	1	***

PHASE II	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.8149	0.4366	0.3783	0.0029
Vancouver Is.	1	***	0.6791	0.6874	0.0421
Fuegians	1	1	***	0.8651	0.0899
Australians	1	1	1	***	0.1588
Bushmen	0.029	0.421	0.899	1	***

Table D8. Descriptive statistics (mean and standard deviation) of relative buccal, lingual and phase II facet areas, within meat-eaters and mixed-diet modern hunter-gatherers.

		Buccal		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD
Meat-eaters	32	48.0	3.5	15.8	7.6	32.4	8.0
Mixed-diet	10	45.5	3.9	25.4	5.7	26.1	5.3

Table D9. Comparison (Mann-Whitney U-test) between meat-eaters and mixed-diet modern hunter-gatherers, considering the relative areas of buccal, lingual and phase II facets. Significant p-values (<0.05) are highlighted in red.

BUCCAL	*Meat-eaters*	*Mixed-diet*
Meat-eaters	0.06711	***
Mixed-diet	***	0.6711

LINGUAL	*Meat-eaters*	*Mixed-diet*
Meat-eaters	0.00143	***
Mixed-diet	***	0.00143

PHASE II	*Meat-eaters*	*Mixed-diet*
Meat-eaters	0.01545	***
Mixed-diet	***	0.01545

Table D10. Comparison (NPMANOVA) between modern hunter-gatherer groups considering the relative areas of buccal, lingual and phase II facets. Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

NPMANOVA	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.5457	0.4229	0.1978	0.0009
Vancouver Is.	1	***	0.6667	0.7306	0.0273
Fuegians	1	1	***	0.4428	0.0056
Australian ab.	1	1	1	***	0.2426
Bushmen	0.009	0.273	0.056	1	***

Table D11. Descriptive statistics (mean and standard deviation) of buccal, lingual, phase II and total facet inclinations (dip angle), within the modern hunter-gatherer groups (wear stage 3).

		Total		**Buccal**		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Inuit	8	18.8	2.6	18.9	3.2	22.5	6.6	17.0	4.4
Vancouver Is.	9	17.2	4.7	17.8	5.0	18.6	6.6	16.3	7.0
Fuegians	7	18.4	1.7	19.2	4.1	25.3	7.7	14.8	6.7
Australian ab.	3	13.3	1.8	13.8	5.8	13.7	4.4	12.2	3.1
Bushmen	6	19.2	3.0	22.6	5.7	22.5	7.2	14.8	2.8

Table D12. Comparison (Permutation t test) between modern hunter-gatherer groups considering the dip angle of buccal, lingual, phase II and total facets (wear stage 3). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

BUCCAL	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.6242	0.8717	0.0859	0.1477
Vancouver Is.	1	***	0.5635	0.2642	0.1068
Fuegians	1	1	***	0.1422	0.2373
Australian ab.	0.859	1	1	***	0.0568
Bushmen	1	1	1	0.568	***

LINGUAL	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.2257	0.4423	0.0651	0.9970
Vancouver Is.	1	***	0.0879	0.2615	0.3014
Fuegians	1	0.879	***	0.0329	0.5123
Australian ab.	0.651	1	0.329	***	0.1050
Bushmen	1	1	1	1	***

PHASE II	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.8112	0.6675	0.5510	0.3278
Vancouver Is.	1	***	0.4523	0.1217	0.2935
Fuegians	1	1	***	0.3675	0.6144
Australian ab.	1	1	1	***	0.9862
Bushmen	1	1	1	1	***

Table D13. Descriptive statistics (mean and standard deviation) of buccal, lingual, phase II and total facet inclinations (dip angle), within meat-eaters and mixed-diet modern hunter-gatherers (wear stage 3).

		Total		**Buccal**		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Meat-eaters	24	18.1	3.3	25.7	4.1	22.1	7.3	16.1	6.0
Mixed-diet	9	17.2	3.9	19.7	6.9	19.6	7.5	13.9	3.0

Table D14. Comparison (Mann-Whitney U-test) between meat-eaters and mixed-diet modern hunter-gatherers (wear stage 3), considering the dip angle of buccal, lingual, phase II and total facets. Significant p-values (<0.05) are highlighted in red.

BUCCAL	*Meat-eaters*	*Mixed-diet*
Meat-eaters	***	0.4546
Mixed-diet	0.4546	***

LINGUAL	*Meat-eaters*	*Mixed-diet*
Meat-eaters	***	0.5853
Mixed-diet	0.5853	***

PHASE II	*Meat-eaters*	*Mixed-diet*
Meat-eaters	***	0.642
Mixed-diet	0.642	***

TOTAL	*Meat-eaters*	*Mixed-diet*
Meat-eaters	***	0.3848
Mixed-diet	0.3848	***

Table D15. Descriptive statistics (mean and standard deviation) of occlusal relief index (ORI), within the modern hunter-gatherer groups (wear stage 3).

		ORI	
	N	Mean	SD
Inuit	8	1.42	0.07
Vancouver Is.	*9*	1.35	0.09
Fuegians	*7*	1.37	0.08
Australian ab.	*3*	1.29	0.07
Bushmen	*6*	1.37	0.06

Table D16. Comparison (Permutation t test) between modern hunter-gatherer groups (wear stage 3), taking into account the occlusal relief index (ORI). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

ORI	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.1343	0.2293	0.0193	0.1920
Vancouver Is.	1	***	0.6601	0.2885	0.6668
Fuegians	1	1	***	0.1221	0.9961
Australian ab.	0.193	1	1	***	0.0823
Bushmen	1	1	1	0.823	***

Table D17. Descriptive statistics (mean and standard deviation) of occlusal relief index (ORI) within meat-eaters and mixed-diet modern hunter-gatherers (wear stage 3).

		ORI	
	N	Mean	SD
Meat-eaters	24	1.38	0.08
Mixed-diet	*9*	1.34	0.07

Table D18. Comparison (Mann-Whitney U-test) between meat-eaters and mixed-diet modern hunter-gatherers (wear stage 3), considering the occlusal relief index (ORI). Significant p-values (<0.05) are highlighted in red.

ORI	*Meat-eaters*	*Mixed-diet*
Meat-eaters	***	0.1889
Mixed-diet	0.1889	***

Table D19. Descriptive statistics (mean, circular standard deviation (CSD) and Rayleigh test (p)) of facet dip directions within the modern hunter-gatherer groups. Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

			LRT			**LPT**			**MT**			**MPT**	
	N	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)
Inuit	10	37.10	11.50	< 1E-12	88.08	24.98	< 1E-12	260.71	34.29	1.76E-04	286.53	42.4	0.001
Vancouver Is.	15	42.16	16.04	6.19E-07	115.93	19.55	7.22E-07	271.07	46.95	1.62E-04	258.82	51.18	5.62E-04
Fuegians	7	43.18	19.87	1.53E-04	101.34	17.85	6.46E-05	238.7	33.69	3.00E-03	307.25	119.14	0.917
Australian ab.	3	47.46	19.92	0.057	129.84	17.54	0.051	256.71	16.85	0.05	247.32	22.55	0.065
Bushmen	7	60.91	15.74	1.73E-06	122.24	13.23	< 1E-12	260.84	27.39	9.67E-04	272.97	54.11	0.051

Table D20. Comparison (Watson-Williams test) between modern hunter-gatherer groups considering LPT, LRT, MT and MPT facet dip directions. Significant p-values (<0.05) are highlighted in red. Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

LRT	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.520	0.465	0.321	0.004
Vancouver Is.		***	0.920	0.716	0.064
Fuegians			***	0.785	0.110
Australian ab.				***	0.335
Bushmen					***

MT	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.5760	0.2340	0.8520	0.9940
Vancouver Is.		***	0.1360	0.6070	0.6120
Fuegians			***	0.4310	0.2280
Australian ab.				***	0.8280
Bushmen					***

LPT	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.0140	0.2700	0.0280	0.0070
Vancouver Is.		***	0.1880	0.3820	0.5420
Fuegians			***	0.0690	0.0390
Australian ab.				***	0.5190
Bushmen					***

MPT	*Inuit*	*Vancouver Is.*	*Fuegians*	*Australian ab.*	*Bushmen*
Inuit	***	0.1960	0.7450	0.1580	0.6020
Vancouver Is.		***	0.4500	0.7030	0.5950
Fuegians			***	0.4240	0.6180
Australian ab.				***	0.4550
Bushmen					***

Table D21. Descriptive statistics (mean, circular standard deviation (CSD) and Rayleigh test (p)) of facet dip directions within meat-eaters and mixed-diet modern hunter-gatherers. Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

			LRT			**LPT**			**MT**			**MPT**	
	N	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)
Meat-eaters	32	40.75	40.75	3.42E-12	104.05	26.34	3.21E-11	259.89	43.4	8.89E-09	272.5	62.96	3.54E-05
Mixed-diet	10	56.95	56.95	< 1E-12	124.48	15.05	< 1E-12	259.54	24.71	< 1E-12	263.21	47.55	0.004

Table D22. Comparison (Watson-Williams test) between meat-eaters and mixed-diet modern hunter-gatherers, considering LPT, LRT, MT and MPT facet dip directions. Significant p-values (<0.05) are highlighted in red. Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

LRT	*Meat-eaters*	*Mixed-diet*
Meat-eaters	***	0.0240
Mixed-diet		***

MT	*Meat-eaters*	*Mixed-diet*
Meat-eaters	***	0.9800
Mixed-diet		***

LPT	*Meat-eaters*	*Mixed-diet*
Meat-eaters	***	0.0240
Mixed-diet		***

MPT	*Meat-eaters*	*Mixed-diet*
Meat-eaters	***	0.6640
Mixed-diet		***

Table D23. Descriptive statistics (mean and standard deviation) of relative buccal, lingual and phase II facet areas, within the Neanderthal ecogeographic groups. Deciduous woodland (DWN); Mediterranean evergreen (MEN); Steppe/Coniferous forest (SCN).

		Buccal		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD
DWN	12	36.5	5.2	34.5	9.1	27.8	5.3
MEN	3	38.0	3.6	29.7	3.8	32.7	4.0
SCN	4	44.5	5.7	18.5	6.4	34.5	4.3

Table D24. Comparison (Permutation t test) between Neanderthal ecogeographic groups considering the relative areas of buccal, lingual and phase II facets. Deciduous woodland (DWN); Mediterranean evergreen (MEN); Steppe/Coniferous forest (SCN). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

BUCCAL	*DWN*	*MEN*	*SCN*
DWN	***	0.6869	0.0251
MEN	1	***	0.1105
SCN	0.0753	0.3315	***

LINGUAL	*DWN*	*MEN*	*SCN*
DWN	***	0.4141	0.0062
MEN	1	***	0.0315
SCN	0.0186	0.0945	***

PHASE II	*DWN*	*MEN*	*SCN*
DWN	***	0.1518	0.0608
MEN	0.4554	***	0.6919
SCN	0.1824	1	***

Table D25. Comparison (NPMANOVA) between Neanderthal ecogeographic groups considering the relative areas of buccal, lingual and phase II facets. Deciduous woodland (DWN); Mediterranean evergreen (MEN); Steppe/Coniferous forest (SCN). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

NPMANOVA	DWN	MEN	SCN
DWN	***	0.3318	0.0076
MEN	0.9954	***	0.0533
SCN	0.0228	0.1599	***

Table D26. Descriptive statistics (mean, circular standard deviation (CSD) and Rayleigh test (p)) of facet dip directions within Neanderthal ecogeographic groups. Deciduous woodland (DWN); Mediterranean evergreen (MEN); Steppe/Coniferous forest (SCN). Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

			LRT			**LPT**			**MT**			**MPT**	
	N	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)
DWN	12	32.96	15.43	1.13E-06	112.31	11.85	1.48E-06	264.42	21.93	< 1E-12	300.54	100.8	0.591
MEN	3	46.8		0.033	115.56		0.033	228.36	38.11	0.149	278.3	32.86	0.112
SCN	4	43.47	7.66	0.008	124.06	8	0.008	228.9	22.8	0.021	257.54	23.29	0.021

Table D27. Comparison (Watson-Williams test) between Neanderthal ecogeographic groups, considering LPT, LRT, MT and MPT facet dip directions. Significant p-values (<0.05) are highlighted in red. Deciduous woodland (DWN); Mediterranean evergreen (MEN); Steppe/Coniferous forest (SCN). Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

LRT	*DWN*	*MEN*	*SCN*
DWN	***	0.174	0.236
MEN		***	0.622
SCN			***

MT	*DWN*	*MEN*	*SCN*
DWN	***	0.085	0.021
MEN		***	0.985
SCN			***

LPT	*DWN*	*MEN*	*SCN*
DWN	***	0.681	0.104
MEN		***	0.299
SCN			***

MPT	*DWN*	*MEN*	*SCN*
DWN	***	0.654	0.367
MEN		***	0.459
SCN			***

Table D28. Descriptive statistics (mean and standard deviation) of relative buccal, lingual and phase II facet areas, within early *Homo sapiens* ecogeographic groups. Mediterranean evergreen (MEHS); Steppe/Coniferous forest (SEHS).

		Buccal		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD
MEHS	7	39.9	4.5	20.1	6.2	38.4	6.3
SEHS	5	45.6	2.5	21.0	4.5	28.0	2.5

BUCCAL	MEHS	SEHS
MEHS	***	0.0323
SEHS	0.0323	***

LINGUAL	MEHS	SEHS
MEHS	***	0.8472
SEHS	0.8472	***

PHASE II	MEHS	SEHS
MEHS	***	0.0083
SEHS	0.0083	***

Table D29. Comparison (Permutation t test) between early *Homo sapiens* ecogeographic groups considering the relative areas of buccal, lingual and phase II facets. Mediterranean evergreen (MEHS); Steppe/Coniferous forest (SEHS). Significant p-values (<0.05) are highlighted in red.

NPMANOVA	MEHS	SEHS
MEHS	***	0.0078
SEHS	0.0078	***

Table D30. Comparison (NPMANOVA) between early *Homo sapiens* from Mediterranean evergreen (MEHS) and Steppe/Coniferous forest (SEHS), considering the relative areas of buccal, lingual and phase II facets. Significant p-values (<0.05) are highlighted in red.

Table D31. Descriptive statistics (mean and standard deviation) of buccal, lingual, phase II and total facet inclinations (dip angle), within early *Homo sapiens* from Mediterranean evergreen (MEHS) and Steppe/Coniferous forest (SEHS) with wear stage 3.

		Buccal		**Lingual**		**Phase II**		**Total**	
	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
MEHS	5	20.26	4.20	28.71	7.01	14.97	5.00	21.07	3.91
SEHS	3	19.65	4.86	26.67	10.42	16.25	2.96	19.19	4.40

BUCCAL	MEHS	SEHS
MEHS	***	0.8836
SEHS	0.8836	***

LINGUAL	MEHS	SEHS
MEHS	***	0.7355
SEHS	0.7355	***

PHASE II	MEHS	SEHS
MEHS	***	0.7346
SEHS	0.7346	***

TOTAL	MEHS	SEHS
MEHS	***	0.5524
SEHS	0.5524	***

Table D32. Comparison (Permutation t test) between early *Homo sapiens* from Mediterranean evergreen (MEHS) and Steppe/Coniferous forest (SEHS), considering the dip angle of buccal, lingual, phase II and total facets (wear stage 3). Significant p-values (<0.05) are highlighted in red.

	N	Mean	SD
MEHS	5	1.32	0.09
SEHS	3	1.40	0.10

Table D33. Descriptive statistics (mean and standard deviation) of occlusal relief index (ORI), within early *Homo sapiens* from Mediterranean evergreen (MEHS) and Steppe/Coniferous forest (SEHS) with wear stage 3.

ORI	MEHS	SEHS
MEHS	***	0.2999
SEHS	0.2999	***

Table D34. Comparison (Permutation t test) between early *Homo sapiens* from Mediterranean evergreen (MEHS) and Steppe/Coniferous forest (SEHS), considering the occlusal relief index (ORI) (wear stage 3). Significant p-values (<0.05) are highlighted in red.

Table D35. Descriptive statistics (mean, circular standard deviation (CSD) and Rayleigh test (p)) of facet dip directions within early *Homo sapiens* from Mediterranean evergreen (MEHS) and Steppe/Coniferous forest (SEHS). Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

		LRT			LPT			MT			MPT		
	N	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)
MEHS	7	39.17	18.71	9.84E-05	118.8	9.7	< 1E-12	260.31	15.03	< 1E-12	249.55	49.32	0.029
SEHS	5	40.42	14.32	0.002	103.93	14.98	0.003	255.89	22.51	0.006	263.52	43.44	0.094

Table D36. Comparison (Watson-Williams test) between early *Homo sapiens* from Mediterranean evergreen (MEHS) and Steppe/Coniferous forest (SEHS), considering LPT, LRT, MT and MPT facet dip directions. Significant p-values (<0.05) are highlighted in red. Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

LRT	MEHS	SEHS
MEHS	***	0.91
SEHS		***

MT	MEHS	SEHS
MEHS	***	0.716
SEHS		***

LPT	MEHS	SEHS
MEHS	***	0.085
SEHS		***

MPT	MEHS	SEHS
MEHS	***	0.667
SEHS		***

Table D37. Descriptive statistics (mean and standard deviation) of relative buccal, lingual and phase II facet areas, within Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG).

		Buccal		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD
NEA	19	38.4	5.8	30.4	1.0	29.9	6.0
EHS	12	42.3	4.7	20.5	5.4	34.1	7.3
MHG	42	47.4	3.7	18.1	8.2	30.9	6.3

BUCCAL	NEA	EHS	MHG
NEA	***	0.08118	3.39E-07
EHS	0.2435	***	0.0017
MHG	1.02E-06	0.0050	***

LINGUAL	NEA	EHS	MHG
NEA	***	0.0017	1.98E-05
EHS	0.0050	***	0.2793
MHG	5.94E-05	0.8379	***

PHASE II	NEA	EHS	MHG
NEA	***	0.1944	0.8213
EHS	0.5831	***	0.1424
MHG	1	0.4273	***

Table D38. Comparison (Mann-Whitney U-test) between Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG), considering the relative areas of buccal, lingual and phase II facets. Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

Table D39. Descriptive statistics (mean and standard deviation) of relative areas of wear facets developed along the four main cusps of M^1 (Hypocone, Protocone, Paracone and Metacone), within Neanderthals (NEA), Middle Paleolithic *Homo sapiens* (MPHS), Upper Paleolithic *Homo sapiens* (UPHS) and modern hunter-gatherers (MHG).

		Hypocone			**Protocone**			**Paracone**			**Metacone**	
	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
NEA	10	21.4	4.4	10	37.8	4.5	10	21.2	2.4	10	18.5	3.1
MPHS	5	23.0	2.5	5	37.2	3.8	5	20.8	1.8	5	17.6	2.6
UPHS	5	20.2	1.1	5	34.2	2.0	5	23.8	1.6	5	21.6	2.8
MHG	20	17.8	5.9	20	34.7	5.1	20	25.9	3.7	20	21.6	3.8

Table D40. Comparison (Permutation t test) between Neanderthals (NEA), Middle Paleolithic *Homo sapiens* (MPHS), Upper Paleolithic *Homo sapiens* (UPHS) and modern hunter-gatherers (MHG), considering relative areas of wear facets developed along the four main cusps of M^1 (Hypocone, Protocone, Paracone and Metacone). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

HYPOCONE M^1	NEA	MPHS	UPHS	MHG
NEA	***	0.4679	0.6242	0.1212
MPHS	1	***	0.0805	0.0862
UPHS	1	0.483	***	0.401
MHG	0.7272	0.5172	1	***

PARACONE M^1	NEA	MPHS	UPHS	MHG
NEA	***	0.7864	0.0582	0.0011
MPHS	1	***	0.0406	0.0095
UPHS	0.349	0.2436	***	0.2498
MHG	0.0066	0.057	1	***

PROTOCONE M^1	NEA	MPHS	UPHS	MHG
NEA	***	0.8411	0.121	0.117
MPHS	1	***	0.1297	0.332
UPHS	0.726	0.7782	***	0.7821
MHG	0.702	1	1	***

METACONE M^1	NEA	MPHS	UPHS	MHG
NEA	***	0.6357	0.0966	0.0365
MPHS	1	***	0.0585	0.0444
UPHS	0.580	0.351	***	0.9637
MHG	0.219	0.2664	1	***

Table D41. Descriptive statistics (mean and standard deviation) of relative areas of wear facets developed along the four main cusps of M^2 (Hypocone, Protocone, Paracone and Metacone), within Neanderthals (NEA), Middle Paleolithic *Homo sapiens* (MPHS) and modern hunter-gatherers (MHG).

		Hypocone			**Protocone**			**Paracone**			**Metacone**	
	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
NEA	9	18.6	4.3	9	43.9	5.6	9	22.0	4.2	9	15.0	5.5
MPHS	2	25.5	3.5	2	30.0	8.5	2	27.0	7.0	2	17.5	2.1
MHG	17	13.9	5.3	22	40.5	7.0	22	27.6	4.7	22	20.2	4.2

Table D42. Comparison (Permutation t test) between Neanderthals (NEA) and modern hunter-gatherers (MHG), considering relative areas of wear facets developed along the four main cusps of M^1 (Hypocone, Protocone, Paracone and Metacone). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

HYPOCONE M^2	NEA	MHG
NEA	***	0.038
MHG	0.038	***

PARACONE M^2	NEA	MHG
NEA	***	0.007
MHG	0.007	***

PROTOCONE M^2	NEA	MHG
NEA	***	0.2069
MHG	0.2069	***

METACONE M^2	NEA	MHG
NEA	***	0.0109
MHG	0.0109	***

Table D43. Descriptive statistics (mean and standard deviation) of buccal, lingual, phase II and total facet inclinations (dip angle in molars with wear stage 2), within Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG).

		Total		**Buccal**		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
NEA	13	27.7	3.2	30.4	4.2	32.5	5.7	23.0	7.0
EHS	5	28.1	4.3	25.9	5.1	31.1	4.7	27.8	12.4
MHG	9	21.0	5.1	22.3	6.3	19.4	6.0	21.4	5.7

Table D44. Comparison (Permutation t test) between Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG), considering dip angle of buccal, lingual, phase II and total facets (in molars with wear stage 2). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

TOTAL	NEA	EHS	MHG
NEA	***	0.8292	0.0237
EHS	1	***	0.0004
MHG	0.0711	0.0012	***

LINGUAL	NEA	EHS	MHG
NEA	***	0.6427	0.0058
EHS	1	***	0.0001
MHG	0.0174	0.0003	***

BUCCAL	NEA	EHS	MHG
NEA	***	0.0679	0.2987
EHS	0.2037	***	0.0025
MHG	0.8961	0.0075	***

PHASE II	NEA	EHS	MHG
NEA	***	0.3121	0.2022
EHS	0.9363	***	0.5842
MHG	0.6066	1	***

Table D45. Descriptive statistics (mean and standard deviation) of buccal, lingual, phase II and total facet inclinations (dip angle in molars with wear stage 3), within Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG).

		Total		**Buccal**		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
NEA	6	20.8	3.3	24.6	4.6	21.3	5.7	17.7	8.0
EHS	8	20.4	3.9	20.0	4.1	27.9	7.8	15.4	4.1
MHG	33	17.8	3.4	18.9	4.9	21.4	7.3	15.5	5.4

Table D46. Comparison (Permutation t test) between Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG), considering dip angle of buccal, lingual, phase II and total facets (in molars with wear stage 3). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

TOTAL	NEA	EHS	MHG
NEA	***	0.8173	0.08
EHS	1	***	0.057
MHG	0.24	0.171	***

LINGUAL	NEA	EHS	MHG
NEA	***	0.1067	0.9714
EHS	0.3201	***	0.0309
MHG	1	0.0927	***

BUCCAL	NEA	EHS	MHG
NEA	***	0.0789	0.0124
EHS	0.2367	***	0.5519
MHG	0.0372	1	***

PHASE II	NEA	EHS	MHG
NEA	***	0.5011	0.969
EHS	1	***	0.4056
MHG	1	1	***

Table D47. Descriptive statistics (mean and standard deviation) of occlusal relief index (ORI) in molars with wear stage 2, within Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG).

		ORI	
	N	Mean	SD
NEA	13	1.50	0.08
EHS	4	1.63	0.05
MHG	9	1.49	0.07

Table D48. Comparison (Permutation t test) between Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG), considering occlusal relief index (ORI) in molars with wear stage 2. Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

ORI	NEA	EHS	MHG
NEA	***	0.0074	0.8422
EHS	0.0222	***	0.0068
MHG	1	0.0204	***

Table D49. Descriptive statistics (mean and standard deviation) of occlusal relief index (ORI) in molars with wear stage 3, within Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG).

		ORI	
	N	Mean	SD
NEA	6	1.34	0.05
EHS	8	1.35	0.10
MHG	33	1.37	0.08

Table D50. Comparison (Permutation t test) between Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG), considering occlusal relief index (ORI) in molars with wear stage 3. Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

ORI	NEA	EHS	MHG
NEA	***	0.7944	0.5635
EHS	1	***	0.346
MHG	1	1	***

Table D51. Descriptive statistics (mean, circular standard deviation (CSD) and Rayleigh test (p)) of facet dip directions within Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG). Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

		LRT			**LPT**			**MT**			**MPT**		
	N	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)
NEA	19	37.43	14.23	4.05E-08	115.31	11.61	3.20E-08	252.06	30.95	2.73E-07	275.96	73.88	0.025
EHS	12	39.70	17.02	8.89E-07	112.68	14.21	1.28E-06	258.51	18.61	5.89E-07	254.94	47.35	0.002
MHG	42	44.59	19.96	< 1E-12	109.14	26.65	< 1E-12	259.79	39.47	1.35E-11	269.83	59.45	1.88E-07

Table D52. Comparison (Watson-Williams test) between Neanderthals (NEA), early *Homo sapiens* (EHS) and modern hunter-gatherers (MHG), considering LPT, LRT, MT and MPT facet dip directions. Significant p-values (<0.05) are highlighted in red. Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

LRT	NEA	EHS	MHG
NEA	***	0.701	0.166
EHS		***	0.447
MHG			***

MT	NEA	EHS	MHG
NEA	***	0.524	0.45
EHS		***	0.91
MHG			***

LPT	NEA	EHS	MHG
NEA	***	0.59	0.316
EHS		***	0.646
MHG			***

MPT	NEA	EHS	MHG
NEA	***	0.409	0.758
EHS		***	0.438
MHG			***

Table D53. Descriptive statistics (mean and standard deviation) of relative buccal, lingual and phase II facet areas, within the human fossil sample (Neanderthals and early *Homo sapiens*) taking into account the ecogeographic variation. Deciduous woodland (DEW); Mediterranean evergreen (MED); Steppe/Coniferous forest (SCF).

		Buccal		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD
DEW	12	36.5	5.2	34.5	9.1	27.8	5.3
MED	10	39.3	4.2	23.0	7.1	36.7	6.1
SCF	9	45.1	4.0	19.9	5.3	30.9	5.6

Table D54. Comparison (Mann-Whitney U-test) between ecogeographic human fossil (Neanderthals and early *Homo sapiens*) groups, considering the relative areas of buccal, lingual and phase II facets. Deciduous woodland (DEW); Mediterranean evergreen (MED); Steppe/Coniferous forest (SCF). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

BUCCAL	DEW	MED	SCF
DEW	***	0.4483	0.0020
MED	1	***	0.0128
SCF	0.0060	0.0383	***

LINGUAL	DEW	MED	SCF
DEW	***	0.0037	0.0002
MED	0.0112	***	0.3913
SCF	0.0005	1	***

PHASE II	DEW	MED	SCF
DEW	***	0.00507	0.2707
MED	0.0152	***	0.0373
SCF	0.812	0.112	***

Table D55. Comparison (NPMANOVA) between ecogeographic human fossil (Neanderthals and early *Homo sapiens*) groups, considering the relative areas of buccal, lingual and phase II facets. Deciduous woodland (DEW); Mediterranean evergreen (MED); Steppe/Coniferous forest (SCF). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

NPMANOVA	DEW	MED	SCF
DEW	***	0.0006	0
MED	0.0018	***	0.0111
SCF	0	0.0333	***

Table D56. Descriptive statistics (mean and standard deviation) of buccal, lingual, phase II and total facet inclinations (dip angle in molars with wear stage 2), within ecogeographic human fossil (Neanderthals and early *Homo sapiens*) groups. Deciduous woodland (DEW); Mediterranean evergreen (MED); Steppe/Coniferous forest (SCF).

		Total		**Buccal**		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
DEW	11	28.1	3.3	31.0	4.1	34.0	4.8	22.1	5.8
MED	2	28.2	5.6	24.0	2.7	32.8	2.1	24.3	2.0
SCF	5	27.1	3.7	27.2	5.1	27.7	5.5	29.3	9.8

Table D57. Comparison (Permutation t test) between human fossils (Neanderthals and early *Homo sapiens*) from deciduous woodland (DEW) and steppe/coniferous forest (SCF), considering dip angle of buccal, lingual, phase II and total facets (in molars with wear stage 2). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

TOTAL	DEW	SCF
DEW	***	0.5922
SCF	0.5922	***

BUCCAL	DEW	SCF
DEW	***	0.1293
SCF	0.1293	***

LINGUAL	DEW	SCF
DEW	***	0.0382
SCF	0.0382	***

PHASE II	DEW	SCF
DEW	***	0.0848
SCF	0.0848	***

Table D58. Descriptive statistics (mean and standard deviation) of buccal, lingual, phase II and total facet inclinations (dip angle in molars with wear stage 3), within human fossils (Neanderthals and early *Homo sapiens*) from Mediterranean evergreen (MED) and steppe/coniferous forest (SCF).

		Total		**Buccal**		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
MED	8	21.2	2.3	23.0	5.0	25.4	7.5	15.8	6.7
SCF	5	20.1	3.8	21.6	4.3	26.6	7.4	16.4	5.5

Table D59. Comparison (Permutation t test) between human fossils (Neanderthals and early *Homo sapiens*) from Mediterranean evergreen (MED) and steppe/coniferous forest (SCF), considering dip angle of buccal, lingual, phase II and total facets (in molars with wear stage 3). Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

TOTAL	MED	SCF
MED	***	0.5904
SCF	0.5904	***

LINGUAL	MED	SCF
MED	***	0.8
SCF	0.8	***

BUCCAL	MED	SCF
MED	***	0.6072
SCF	0.6072	***

PHASE II	MED	SCF
MED	***	0.6438
SCF	0.6438	***

	N	ORI Mean	SD
DEW	11	1.50	0.08
MED	2	1.62	0.03
SCF	4	1.56	0.10

Table D60. Descriptive statistics (mean and standard deviation) of occlusal relief index (ORI) in molars with wear stage 2, within ecogeographic human fossil (Neanderthals and early *Homo sapiens*) groups. Deciduous woodland (DEW); Mediterranean evergreen (MED); Steppe/Coniferous forest (SCF).

ORI	DEW	SCF
DEW	***	0.269
SCF	0.269	***

Table D61. Comparison (Permutation t test) between human fossils (Neanderthals and early *Homo sapiens*) from deciduous woodland (DEW) and steppe/coniferous forest (SCF), considering occlusal relief indexes (ORI) in molars with wear stage 2. Significant p-values (<0.05) are highlighted in red.

	N	ORI Mean	SD
MED	8	1.33	0.08
SCF	5	1.38	0.08

Table D62. Descriptive statistics (mean and standard deviation) of occlusal relief index (ORI) in molars with wear stage 3, within human fossil (Neanderthals and early *Homo sapiens*) from Mediterranean evergreen (MED) and steppe/coniferous forest (SCF).

ORI	MED	SCF
MED	***	0.316
SCF	0.316	***

Table D63. Comparison (Permutation t test) between human fossils (Neanderthals and early *Homo sapiens*) from Mediterranean evergreen (MED) and steppe/coniferous forest (SCF), considering occlusal relief indexes (ORI) in molars with wear stage 3. Significant p-values (<0.05) are highlighted in red.

Table D64. Descriptive statistics (mean, circular standard deviation (CSD) and Rayleigh test (p)) of facet dip directions within ecogeographic human fossil (Neanderthals and early *Homo sapiens*) groups. Deciduous woodland (DEW); Mediterranean evergreen (MED); Steppe/Coniferous forest (SCF). Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

			LRT			**LPT**			**MT**			**MPT**	
	N	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)	Mean	CSD	R (p)
DEW	12	33.0	15.4	1.13E-06	112.3	11.8	1.48E-06	264.4	21.9	< 1E-12	300.5	10.4	0.591
MED	10	41.5	16.3	< 1E-12	117.8	9.4	< 1E-12	252.3	28.7	2.02E-05	259.2	47.5	0.004
SCF	9	47.8	11.9	< 1E-12	113.0	15.9	< 1E-12	243.9	26.3	3.45E-05	260.2	33.9	0.001

Table D65. Comparison (Watson-Williams test) between ecogeographic human fossil (Neanderthals and early *Homo sapiens*) groups, considering LPT, LRT, MT and MPT facet dip directions. Deciduous woodland (DEW); Mediterranean evergreen (MED); Steppe/Coniferous forest (SCF). Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT). Significant p-values (<0.05) are highlighted in red.

LRT	DEW	MED	SCF
DEW	***	0.241	0.189
MED	1.461	***	0.971
SCF	1.860	0.001	***

MT	DEW	MED	SCF
DEW	***	0.294	0.079
MED	1.159	***	0.538
SCF	3.437	0.395	***

LPT	DEW	MED	SCF
DEW	***	0.269	0.916
MED	1.294	***	0.450
SCF	0.011	0.597	***

MPT	DEW	MED	SCF
DEW	***	0.312	0.325
MED	1.077	***	0.959
SCF	1.025	0.003	***

Table D66. Descriptive statistics (mean and standard deviation) of relative buccal, lingual and phase II facet areas, within Neanderthals (DWN, MEN and SCN), early *Homo sapiens* (MEHS and SEHS) and modern hunter-gathers (Meat-eaters and Mixed-diet) groups.

		Buccal		**Lingual**		**Phase II**	
	N	Mean	SD	Mean	SD	Mean	SD
DWN.	12	37.5	5.2	34.5	9.1	27.8	5.3
MEN.	3	38.0	3.6	34.0	3.8	32.7	4.0
SCN	4	44.5	5.7	18.5	6.5	34.5	6.6
MEHS	7	48.0	4.5	20.1	6.2	38.4	6.3
SEHS	5	45.6	2.5	21.0	4.5	28.0	2.5
Meat-eaters	32	48.0	3.5	15.8	7.6	32.4	8.1
Mixed-diet	10	45.5	3.9	25.4	5.7	26.1	5.4

Table D67. Comparison (Permutation t test) between Neanderthals (DWN, MEN and SCN), early *Homo sapiens* (MEHS and SEHS) and modern hunter-gathers (Meat-eaters and mixed-diet) groups, considering the relative areas of buccal, lingual and phase II facets. Uncorrected p-values on the left; corrected p-values (Bonferroni) on the right. Significant p-values (<0.05) are highlighted in red.

	Uncorrected		Bonferroni cor.	
BUCCAL	*Meat-eaters*	*Mixed-diet*	*Meat-eaters*	*Mixed-diet*
DWN	0.0001	0.0001	0.001	0.001
MEN.	0.0001	0.0094	0.001	0.094
SCN	0.0822	0.7169	0.822	1
MEHS.	0.0001	0.0185	0.001	0.185
SEHS	0.1366	0.9784	1	1

	Uncorrected		Bonferroni cor.	
LINGUAL	*Meat-eaters*	*Mixed-diet*	*Meat-eaters*	*Mixed-diet*
DWN	0.0001	0.0069	0.001	0.069
MEN.	0.0031	0.2838	0.031	1
SCN	0.5039	0.0673	1	0.673
MEHS.	0.1736	0.0917	1	0.917
SEHS	0.1541	0.1478	1	1

	Uncorrected		Bonferroni cor.	
PHASE II	*Meat-eaters*	*Mixed-diet*	*Meat-eaters*	*Mixed-diet*
DWN	0.068	0.4983	0.68	1
MEN.	0.9647	0.0802	1	0.802
SCN	0.6272	0.0277	1	0.277
MEHS.	0.074	0.0006	0.74	0.006
SEHS	0.2448	0.4805	1	1

Table D68. Comparison (NPMANOVA) between Neanderthals (DWN, MEN and SCN), early *Homo sapiens* (MEHS and SEHS) and modern hunter-gathers (meat-eaters and mixed-diet) groups, considering the relative areas of buccal, lingual and phase II facets. Uncorrected p-values above the diagonal; corrected p-values (Bonferroni) below the diagonal. Significant p-values (<0.05) are highlighted in red.

NPMANOVA	*NEA def*	*NEA med*	*NEA ste*	*EHS med*	*EHS ste*	*Meat-eaters*	*Australians*	*Bushmen*
NEA def	***	0.3219	0.0074	0.0016	0.0056	0	0.0267	0.0243
NEA med	1	***	0.0563	0.0855	0.0158	0.0036	0.1002	0.0975
NEA ste	0.2072	1	***	0.503	0.3138	0.4786	0.7402	0.0319
EHS med	0.0448	1	1	***	0.0074	0.0038	0.0606	0.0038
EHS ste	0.1568	0.4424	1	0.2072	***	0.1611	0.81	0.1781
Meat-eaters	0	0.1008	1	0.1064	1	***	0.4946	0.0016
Australians	0.7476	1	1	1	1	1	***	0.2407
Bushmen	0.6804	1	0.8932	0.1064	1	0.0448	1	***

Table D69. Comparison (Watson-Williams test) between Neanderthals (DWN, MEN and SCN), early *Homo sapiens* (MEHS and SEHS) and modern hunter-gathers (meat-eaters and mixed-diet) groups, considering LPT, LRT, MT and MPT facet dip directions. Significant p-values (<0.05) are highlighted in red. Lateroretrusion (LRT); Lateroprotrusion (LPT); mediotrusion (MT); medioprotrusion (MPT).

LRT	Meat-eaters	Mixed-diet	DWN	MEN	SCN	MEHS	SEHS
Meat-eaters	***	0.024	0.215	0.707	0.673	0.846	0.971
Mixed-diet		***	0.004	0.176	0.141	0.084	0.118
DWN			***	0.172	0.132	0.469	0.395
MEN				***	0.988	0.627	0.674
SCN					***	0.585	0.632
EMEHS						***	0.910
SEHS							***

LPT	Meat-eaters	Mixed-diet	DWN	MEN	SCN	MEHS	SEHS
Meat-eaters	***	0.024	0.298	0.167	0.082	0.148	0.992
Mixed-diet		***	0.056	0.643	0.847	0.419	0.036
DWN			***	0.215	0.067	0.26	0.268
MEN				***	0.683	0.773	0.102
SCN					***	0.415	0.031
EMEHS						***	0.085
SEHS							***

MT	Meat-eaters	Mixed-diet	DWN	MEN	SCN	MEHS	SEHS
Meat-eaters	***	0.980	0.722	0.137	0.128	0.979	0.833
Mixed-diet		***	0.643	0.083	0.091	0.945	0.797
DWN			***	0.029	0.031	0.679	0.504
MEN				***	0.955	0.065	0.203
SCN					***	0.078	0.222
EMEHS						***	0.716
SEHS							***

MPT	Meat-eaters	Mixed-diet	DWN	MEN	SCN	MEHS	SEHS
Meat-eaters	***	0.664	0.432	0.883	0.903	0.363	0.768
Mixed-diet		***	0.359	0.590	0.784	0.601	0.991
DWN			***	0.589	0.475	0.258	0.459
MEN				***	0.750	0.327	0.648
SCN					***	0.437	0.822
EMEHS						***	0.667
SEHS							***

Zusammenfassung

Die Neandertaler (*Homo neanderthalensis*) lebten in Westeurasien zwischen 200.000 bis 30.000 Jahren vor unserer Zeit. Im späten Pleistozän. Sie bewohnten unterschiedliche Lebensräume die von klimatischen Veränderungen geprägt waren.

Viele Untersuchungen haben sich mit der Nahrungsgrundlage der Neandertaler befasst und es wurde oft diskutiert, ob die Neandertaler eher Aasfresser oder aktive Jäger waren. Die Analyse der Begleitfaunen an den Fundstellen der gefundenen Steinwerkzeuge und die Isotopenzusammensetzung von Knochen und Zähnen, haben zu der Hypothese geführt, dass die Neanderthaler tatsächlich aktive Jäger waren. Sie haben sich wahrscheinlich vorwiegend von tierischen Proteinen von großen bis mittelgroßen Pflanzenfressern ernährt. Das Erscheinen von *Homo sapiens* in Europa während des Sauerstoffisotopenstadiums 3 (OIS3) hat wahrscheinlich infolge der Lebensraumveränderungen einen starken Konkurrenzkampf um die knappen Fleischressourcen zwischen den Neandertalern und *Homo sapiens* ausgelöst. Eine höherentwickelte Werkzeugtechnologie in Verbindung mit komplexeren Sozialstrukturen und einer guten Ausnutzung abwechslungsreicherer Nahrungsquellen (inklusive pflanzlicher Nahrung, Kleinsäuger und anderer Tiere) hat vermutlich den Bevölkerungszuwachs der frühen H*omo sapiens* Populationen in Europa gefördert. Diese wiederum haben im Laufe der Zeit die Neandertaler Populationen in Europa (zusehend) ersetzt.

Die Möglichkeiten der detaillierten Nahrungsrekonstruktion sind sehr begrenzt. Typischerweise sind Knochen besser fossil erhaltben als pflanzliche Überreste. Dies lässt den Eindruck entstehen, dass Fleisch die Hauptnahrung gewesen ist, denn an den Neandertaler Fundorten wurden z.T. größere Mengen von Knochenresten gefunden, die z.B. Bearbeitungsspuren zeigen.. Deshalb ist es durchaus möglich, dass Untersuchungen eher dazu neigen, den Konsum tierischer Nahrung über zu bewerten und den Konsum pflanzlicher Nahrung zu unterschätzen. Isotopenanalysen von Knochenkollagen (das weitgehend aus Proteinen besteht) zeigen, dass tierische Proteine konsumiert wurden, aber die Ergebnisse lassen nicht direkt den Schluss zu, dass dies der Hauptbestandteil der Nahrung war. Da tierische Nahrungsquellen sehr proteinreich sind, ist tierische Nahrung durch das Knochenkollagen überrepräsentiert, während der Anteil von Proteinen aus pflanzlicher Nahrung geringer ist, und deshalb ist die Menge pflanzlicher Kost nur schwer abzuschätzen.. Neue Untersuchungen aus Neandertaler Fundregionen in Südeuropa und dem Nahen Osten zur sogenannten „Microwear“, den Mikrospuren der Zahnabnutzung zeigen, dass die Neandertaler unterschiedliche Nahrung verwertet haben; inklusive

Pflanzenmaterial und Meerestiere. Dies steht nun im Widerspruch zu den Ergebnissen, die man von den tierischen Überresten und aus den Isotopenanalysen gewonnen hat.

In der vorliegenden Untersuchung wurden nun erstmals die okklusalen Abnutzungsmuster von Oberkieferbackenzähnen von Neandertalern und frühen *Homo sapiens* analysiert, die aus unterschiedlichen geografischen Gebieten und aus unterschiedlichen Zeiträumen stammen. Hierfür wurde eine zerstörungsfreie Methode angewendet, die auf der digitalen Analyse von dreidimensionalen virtuellen Zahnmodellen basiert. Die Computermodelle wurden mit daten aus Oberflächenscans von Zahnabgüssen rekonstruiert.

Die grobe Zahnabnutzung verändert das Kronenrelief langsam, im Gegensatz zu den Mikro-Zahnabnutzungsmustern, die schnell entstehen und sich von Mahlzeit zu Mahlzeit verändern können.Während der Lebenszeit eines Individuums wird die Nahrungsbeschaffenheit über einen langen Zeitraum in das grobe Reliefmuster eingraviert und reflekiert somit das gesamte Nahrungsspektrum.

Die Oberfläche von Zahnabgüssen wurde mit einem Streifenlicht-Scanning System (smartSCAN 3D, Breuckmann GmbH) mit einer x-y Auflösung von 55µm erfasst. Zur Erfassung und Ausrichtung der Scandaten in Form von Punktwolken wurde die Software optpCAT (Breuckmann, GmbH) eingesetzt. Die weitere Bearbeitung und Quantifizierung erfolgte mit PolyWorks® 10.1 (InnovMetric Software Inc.).

Die dreidimensional digitalen Zahnmodelle wurden mit der sogenannten „Occlusal Fingerprint Analysis“ Methode (OFA) untersucht. Diese Technik beschreibt und quantifiziert das okklusale Abnutzungsmuster des Kronenreliefs mittels zweier Winkel, die Neigung und Neigungsrichtung der Kontaktfacetten, sowie deren Flächen und Umfänge. Vor der Analyse der Okklusalflächen musste jedes Polygonmodell exakt ausgerichtet werden. Die OFA-Methode erlaubt durch die Rekonstruktion der Unterkieferbewegung, die für den Kontakt beim Kauvorgang verantwortlich ist, die Extraktion von Informationen über die Dynamik der okklusalen Beziehungen und ihrer Funktionen. Da die Kieferbewegung und Nahrungszusammensetzung in Zusammenhang stehen, können die gewonnenen Ergebnisse zur Interpretation des Nahrungsspektrums der beiden pleistozänen Hominiden herangezogen werden.

Um zu bewerten, wie sehr unterschiedliche Nahrung die okklusalen Abnutzungsmuster beeinflusst, wurde die Stichprobe durch obere Backenzähne von modernen Jägern und Sammlern, deren Nahrungsspektrum bekannt ist, erweitert. Die Ergebnisse der modernen Gruppen wurden dann mit der Stichprobe der Neandertaler und des frühen *Homo sapiens* verglichen. Die Bezahnung von modernen

Jägern und Sammlern, die sich besonders von tierischem Protein ernähren, wie z.B. Inuit, Vancouver Insulaner und Feuerländer wurde genauso untersucht, wie australische Aborigines und afrikanische Buschmänner, die eher Gemischtköstler sind. Falls sich Neandertaler tatsächlich nur von tierischem Eiweiß ernährt haben, wie aus den vorangegangenen Untersuchungen vermutet, sollten sie ein ähnliches Abnutzungsmuster aufweisen, wie die oben genannten modernen Fleischkonsumenten. Wenn sich die Oberflächenabnutzung von Neandertalern und den frühen *Homo sapiens* aber auch von denen moderner Jäger-Sammler und unterscheiden, müssen die möglichen Gründe dafür gefunden werden. Liegt dieser Unterscheid an der unterschiedlichen Zahnmorphologie der beiden Spezies oder liegt es am unterschiedlichen Nahrungsspektrum? Sind die Neandertalerzähne von gleichförmigem Abnutzungsmuster gekennzeichnet? Falls nicht, beziehen sich diese Unterschiede dann auf die ökologisch-geografischen Varianten der Neandertaler in Westeurasien während des mittleren und späten Pleistozän?

Die im Schlussbiss berechneten okklusalen Abnutzungsmuster zeigen durch die Neigungswinkel der Kontaktfacettenden die funktionellen Werkzeuge, die für die unterschiedliche Nahrungsaufbereitung während des Kauzyklus nötig sind. Die „scherenden“ Phase 1 Facetten (beide bukkal und lingual) zeigen in der Regel steilere Flächen als die der „mahlenden“ Phase 2 Facetten. Die Flächen der Phase 2 zeigen eher „quetschende“ Facetten die flacher angelegt sind. Die okklusalen Abnutzungsmuster der Fleischkonsumenten unter den Jägern und Sammlern unterscheiden sich von den Gemischtköstlern. Besonders die Analyse der jeweiligen Facettenflächen zeigen klare Unterschiede zwischen den Fleischkonsumenten und den Gemischtköstlern. Der Okklusale Reliefindex (ORI) und der Neigungswinkel der Abnutzungsfacetten zeigt mehr die Abnutzung in Bezug auf die Nahrung und die Beeinflussung durch äußere Einwirkungen bei der Nahrungszubereitung. Die starke Entwicklung der bukkalen Phase 1 Facetten, zu sehen bei den Fleischkonsumenten der modernen der Jäger und Sammler Gruppen, entsteht wahrscheinlich durch grobe und faserige Fleischnahrung die nur durch eine starke initiale Vertikalkomponente beim Kauen zerkleinert wird. Während die großen lingualen Phase 1 Facetten, zu sehen bei den Gemischtköstlern, eher auf eine omnivore Nahrung zurückzuführen sind, da die Kaubewegungen zur Aufbereitung des Pflanzenmaterials stärker lateral verlaufen. Die Phase 2 Facetten zeigen hingegen weniger ausgeprägte Unterschiede zwischen den Fleischkonsumenten und den Gemischtköstlern. Die Untersuchung der Neigungswinkel der Facettenabhänge zeigen einen signifikanten Unterschied bei den lateroretrusiven (LRT) und lateroprotrusiven (LPT) Facetten zwischen den Fleisch- und den Gemischtköstlern, wohingegen die Untersuchung der modiotrusiven (MT) und medioprotrusiven (MPT) Bewegungen eine große Variabilität aufweist, verursacht durch eine merkliche Überlappung zwischen den Proben aus beiden Nahrungsgruppen. Die hohe Variabilität in den Phase 2 Bewegungen (MT und MPT) ist meist bezogen auf die Abhangneigung von Facetten 10 und 11. Als wesentliches Ergebnis der Untersuchung bleibt festzustellen, dass das okklusale Abnutzungsmuster der Neandertaler sich durch eine ökogeografische Variation charakterisiert. Dadurch ist es möglich drei Hauptgruppen zu unterscheiden, die drei verschiedene Lebensräume bewohnt haben: laubwechselnde Waldgebiete, mediterrane immergrüne Gebiete und steppenartige Gebiete mit Koniferenwäldern. Die Neandertaler aus dem laubwechselnden Waldgebiet (DWN= deciduous woodlands Neanderthals) zeigen in ihrem Abnutzungsmuster eine Reduktion der buccalen Phase 1 Facetten und eine Vergrößerung der lingualen Phase 1 Facetten, mit signifikantem Unterschied zu den Fleischkonsumenten moderner Jäger und Sammler. Dieser Abnutzungsmustertyp, verbunden mit einer hohen Variabilität, deutet auf unterschiedliche und flexible Nahrungsquellen inklusive pflanzlicher Kost hin. Die mediterranen Neandertaler (MEN) zeigen ein ähnliches Abnutzungsmuster wie die DWN. Dagegen besitzen die Neandertaler der Steppe/Koniferenwälder (SCN= steppe/coniferous forest Neanderthals) ein deutlich anderes Abnutzungsmuster, dass durch eine eingeschränkte Variabilität gekennzeichnet ist und denen der Fleischkonsumenten der modernen Jäger und Sammler sehr ähnelt (markante bukkale Phase 1 Facetten und reduzierte linguale Phase 1 Facetten). Das lässt auf ein eingeschränktes Nahrungsspektrum schließen, das wahrscheinlich meist aus tierischem Protein bestand. Die Stichproben der frühen *Homo sapiens* sind in zwei Gruppen eingeteilt worden: Bewohner eines mediterranen Lebensraumes (MEHS= Mediterranean environments *Homo sapiens*) und Bewohner der Steppe / Koniferenwälder (SEHS= steppe environments *Homo sapiens*). Die MEHS zeigen ein Abnutzungsmuster mit gut entwickelten bukkalen Phase 1 Facetten und großen Phase 2 Facetten, das weist auf eine Ernährung mit tierischer und pflanzlicher Kost hin, wie bei den MEN. Ungewöhnlich hinsichtlich der fossilen Tierreste, den stabilen Isotopen und den Zahn "Microwear" Untersuchungen, da diese für *Homo sapiens* aus dem Spätpaläolithikum ein breiteres Nahrungsspektrum erwarten lassen. Die Abnutzungsmuster der SEHS zeigen große Ähnlichkeit mit denen der SCN und den fleischkonsumierenden Jägern und Sammlern, was auf eine bevorzugte Ernährung mit tierischen Proteinen schließen lässt.

Die Entwicklung der Abnutzungsfacetten entlang der Flanken der vier Haupthöcker in den ersten und zweiten oberen Molaren, weisen auf eine klare Beziehung zwischen Zahnmorphologie und Zahnabnutzung hin. Dies zeigt sich an den großen Facetten des Hypokonus in den

Neandertalermolaren und dem gut entwickelten Metakonus wie er beim modernen *Homo sapiens* zu sehen ist. Die Unterschiede, die sich zwischen den ersten Oberkiefermolaren der Neandertaler, mittel- und spätpaläolithischen *Homo sapiens* und den modernem Jägern und Sammlern fanden, waren nicht signifikant. Facetten, die sich entlang der Hypokonus-, Parakonus- und Metakonushöcker der M^2 entwickeln, zeigen einen signifikanten Unterschied zwischen Neandertalern und modernen *Homo sapiens* Gruppen.

Die Variabilität innerhalb der Neandertaler, frühen *Homo sapiens* und modernen Jäger-Sammler-Gruppen, und die Ähnlichkeit der Proben, die zu unterschiedlichen taxonomischen Gruppen gehören die gleiche Lebensräume bewohnten, lassen vermuten, dass die okklusalen Abnutzungsmuster der fossilen Hominiden stark an den Lebensraum und die entsprechenden Nahrungsquellen gekoppelt sind. Die Untersuchung der Neigungswinkel der Facetten und des okklusalen Reliefs zeigten weder eine deutliche Unterscheidung zwischen Neandertalern und frühen *Homo sapiens*, noch zwischen den fossilen Stichproben, die unterschiedliche Lebensräume bewohnten.

Vergleicht man allerdings die Proben der gesamten fossilen Gruppe mit den modernen Jäger-Sammler Gruppen, so findet man einen bemerkenswerten Unterschied. Sowohl bei Neandertalern als auch bei frühen *Homo sapiens* werden steile Abriebfacetten und hohe okklusale Reliefindexwerte gemessen, wohingegen moderne Jäger-Sammler eine flache okklusale Oberfläche aufweisen. Wie bereits erwähnt, der Gebrauch moderner Nahrungszubereitungsformen (z.B. Trocknung, Räuchern oder Einfrieren) beeinflusst die Aufnahme exogener Materialien wie Staub, Asche oder Staubkörner und somit die Abriebwirkung dieser Ernährungsweise. Die komplexeren Zahnreliefbeschaffenheiten bei Neandertalern und frühen *Homo sapiens* können auf die einfachere Nahrungszubereitung und auf die niedrigeren Abriebeigenschaften der konsumierten Nahrung zurückgeführt werden. Darüber hinaus weisen Zahnschmelzsplitterungen an Oberkiefermolaren bei modernen Jäger-Sammlern, im Speziellen bei Inuit, Vancouver Insulaner und Feuerländer, die bei Neandertalern und frühen *Homo sapiens* nicht zu finden sind, ebenso auf einen Unterschied in den Nahrungsgewohnheiten und Kauaktivitäten zwischen den modernen und den fossilen Proben hin.

Das Ergebnis der vorliegenden Untersuchung zeigt, dass das Abnutzungsmuster des Neandertalergebisses von einer ökogeografischen Variation und damit von unterschiedlichen Nahrungsquellen gekennzeichnet ist. Besonders Neandertaler die ein relativ warmes Gebiet in Südeuropa und im Nahen Osten bewohnten, zeigen ein unterschiedliches Abnutzungsmuster zu den

Fleischkonsumenten bei den modernen Jägern und Sammlern, weisen aber einige Ähnlichkeiten mit afrikanischen Buschmänner auf.

Diese Ergebnisse lassen eine große Vielseitigkeit und Flexibilitätund im Nahrungsspektrum vermuten. Im Gegensatz dazu hat die Analyse des Zahnabriebmusters der Neandertaler und frühen *Homo sapiens*, die Europa während des Sauerstoffisotopenstadiums 3 (OIS3) bewohnten, viele Ähnlichkeiten zwischen den beiden Gruppen gezeigt. Das weist auf ähnliche Methoden in der Nahrungsaufbereitung hin und auf Nahrungsquellen, die meist auf tierischem Protein basieren, wie es sich in der Ähnlichkeit mit dem Abnutzungsmuster der Fleischkonsumenten unter den modernen Jägern und Sammlern wiederspiegelt. Die Neandertaler und der frühe *Homo sapiens* waren während der Eiszeiten vermutlich starke Nahrungskonkurrenten.

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