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Analysis of Neanderthal Biodistance using Non-Metric Features of the Dentition

by

Michel Claude Tchang

A Thesis

Submitted to the Graduate Faculty of

St. Cloud State University

in Partial Fulfillment of the Requirements

for the Degree

Master of Science in

Special Studies: Interdisciplinary Neanderthal Studies

May, 2017

Thesis Committee:
Matthew Tornow, Chairperson
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Joseph Melcher
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Abstract

The Neanderthals lived in small communities of hunters and gatherers and were present in a large geographical area extending from Portugal to Siberia. This expansive range implies that Neanderthals lived in a great diversity of climatic conditions. Paleoanthropologists agree, in their observations, that there are differences between European and Middle Eastern Neanderthals, and that this variation covers an east to west cline. Research based on mtDNA simulation has defined three subgroups, a Western subgroup, a Southern subgroup and an Eastern subgroup. This study of Neanderthal biodistance, based on non-metric features of the dentition, aims to address the dental character variability among Neanderthals. This point would permit to determine the presence of Neanderthal subgroups, and, if so, the existence of an east to west cline. From the dental data and the subgroup distribution, the Neanderthal population emigration can be estimated. Results of this research indicate that there is variation in the frequencies of Neanderthal dental characters, the molars showing the most variation, and that this variation can be used to identify four Neanderthal subgroups. This variation is consistent with an east to west, clinal distribution of Neanderthals, and provides evidence of movement patterns within this species.

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Chapter 1: Introduction

In August 1856, several bones, and among them a cranium, were excavated near Düsseldorf, Germany by quarrymen in the Neander Valley (Neander Thal or Tal- in modern German). Scholars such as Virchow and Boule, did not know exactly what kind of creature it was and controversies were ongoing. The cranium had prominent brow ridges, angled cheekbones and a wide nose, and the post cranial bones were more robust with long clavicles, a barrel shaped rib-cage, and large, wide shoulder blades. The kneecaps were large, and the legs had bowed femora and short tibiae. The skeletal description gave the impression of a stumpy and robust creature (Jaubert and Maureille 2012). Charles Darwin's (1859) "The Origin of the Species," helped spread the information of the Neanderthal discovery, and in 1864, King proposed to call this creature *Homo neanderthalensis* (Toussaint et al. 2011).

In 1880, the lower jaw of a young Neanderthal child was found and among cultural debris, including hearths, Mousterian tools, and animal bones at Šipka Cave near Štramberk, in the present day Czech Republic. Following this discovery, the Neanderthal was finally accepted as an ancient human relative. The discovery of a burial in 1908, gave the Neanderthals a more "human" dimension, but its significant was not fully recognized by Boule (1912), who was responsible of the investigation. Boule published the first complete analysis of a Neanderthal in an article in "Annales de Paléontologie" and he described the creature as a brutish old man, with a forward- thrusting head, bent knees and not completely bipedal. For Boule, the low vaulted cranium and large eye brow ridge were to be compared with the large apes such as gorillas, and as such the creature was probably a primitive early human with a corresponding lack of intelligence. In 1909 and 1910 two burials were found in

La Ferrassie, France, and an additional burial was found in La Quina, France in 1911. After World War I, more archaeological digs were done and discoveries showed that the Neanderthal not only controlled fire but also produced and used stone tools, such as blades and scrapers, sophisticated as those used by early humans.

In 1930, the first Neanderthal outside of Europe was found in Tabun, in present day Israel (Stefan and Trinkaus 1998). Later, in 1938 in Teshik-tash (present day Uzbekistan) a Neanderthal child was discovered; in Shanidar (present day Iraq) excavations between 1953-1957 exposed several burials, one of which was filled with pollen and seed, indicating the presence of flowers (Toussaint et al., 2011); at La Chaise de Vouthon (France) the abbots Bourgeois and Delaunay did some research as early as 1850 by but it wasn't until 1930 that systematic digs were done by P. David and several human remains were discovered (David and Bordes 1950). In 1967, A. Debenath (1967) took over the digs and discovered more human remains (Condemi 2001). Between 1983 and 1987 in Fate (Italy), Echassoux et al. (1989) found Neanderthal remains in the collection of a scholar Amerano (1891) who excavated them in the Fate cave in 1891 (Patou-Mathis 2006). Slowly a geographic (and temporal) expansion in Neanderthal sites yielded variation in characters, and began to provide a model of Neanderthal evolution and dispersal.

Since World War II researchers have divided in two opposing groups regarding the species status of Neanderthals and their relations to modern human. One group of scholars (e.g., Trinkaus 1983; Frayer 1992; Wolpoff and Caspari 1997) included Neanderthals within *Homo sapiens*, while others (e.g., Hublin et al. 1996; Bermudez de Castro et al. 1997; Tattersall 1998) viewed Neanderthals as a distinct species. Apart from these opposing views, continued field research has resulted in the recovery of Neanderthals from different Western and Near East countries.

The oldest Neanderthal characters (Table 1.1) are present on a 450,00-year-old *Homo heidelbergensis* specimen, called the Mauer mandible in reference to the site in Germany where it was found (Rosa and Bermudez de Castro. 1998; Rosas et al. 2008; Smith et al. 2010; Peretto et al. 2015). Additional Neanderthal characteristics accumulate over a 250,000 year time span, and by 200,000 years, practically all Neanderthal characters are fully defined. Thus, full "Neanderthalization," in which the suite of Neanderthal characters developed, occurred over 250,000 year process. These characters developed and persisted until the disappearance of Neanderthals, roughly 35,000 years ago, and span a series of Pleistocene glacial interludes and interglacials, identified by the proportions of oxygen isotopes, and referred to as oxygen isotope stages (OIS). The 250,000 year process of Neandethalization occurs between OIS 12 and OIS 7, and the traits persist until the extinction of the Neanderthals during OIS 3.

Table 1.1

Examples of the Oldest Neanderthal Characters (Rosas et al. 2008)

Characters	Description
Bucco-lingual incisors	Large
Premolars morphology	The premolars tend to possess a small, mesiolingually displaced occlusal polygon. P_3 has a large buccal cusp.
Mental foramen position	A posteriorly position, at the level of M_1
Retromolar gap	It is found in some Neanderthals because of the midfacial prognathism

Neanderthals covered large portions of Europe and Asia, ranging from Portugal, in the west, to Siberia, in the east (Figure 1.2). Thus, it is probable that Neanderthals were divided into small populations, separated from each other by several miles (Sanchez-Quinto and Lalueza-Fox 2015), and isolated from one another, by natural obstacles such as the Rhine or Danube Rivers, and the Pyreneans, the Alps or the Ural mountain ranges. These geographic barriers, combined with the cycles of Pleistocene climatic change due to the cycles of glaciation and warm periods (Table 1.2 and Figure 1.1), almost certainly influenced Neanderthal migration and dispersal.

Table 1.2

Warm and Cold Cycles

OIS 3	60,000	warmer		OIS 6	190,000	cooler
OIS 4	74,000	cooler		OIS 7	244,000	warmer
OIS 5	130,000	warmer		OIS 8	301,000	cooler
OIS 5a	85,000	warmer		OIS 9	334,000	warmer
OIS 5b	93,000	cooler		OIS 10	364,000	cooler
OIS 5c	106,000	warmer		OIS 11	427,000	warmer
OIS 5d	115,000	cooler				
OIS 5e	130,000	warmer				

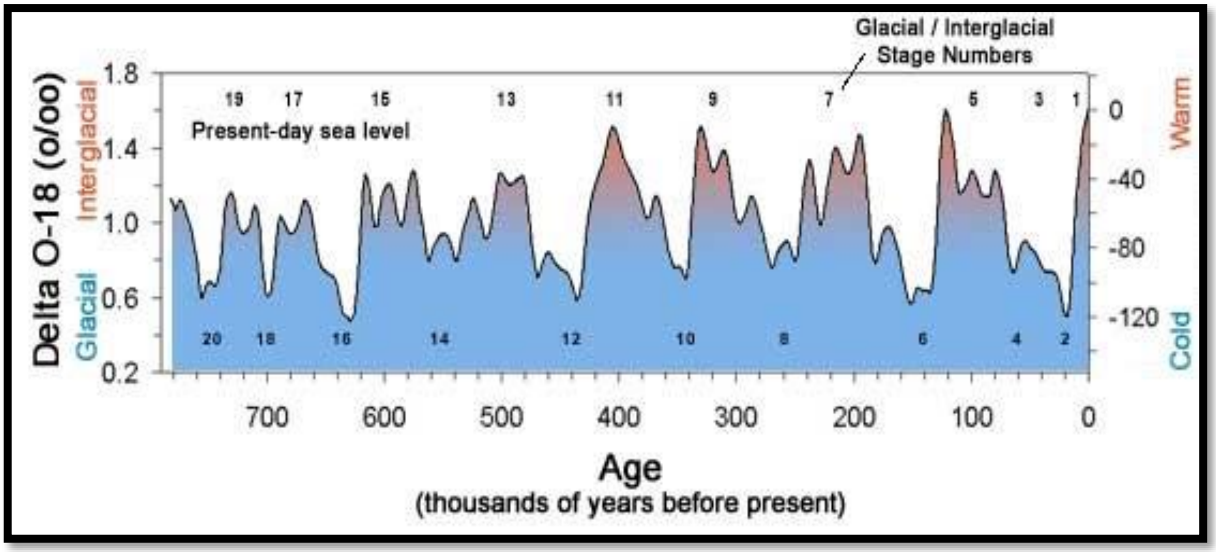


Figure 1.1. OIS periods from 800,000 years ago. It is to note that Neanderthals survived several cycles of glaciation and warm periods. (modified from Imbrie 1984)

Climatic changes during the mid to late Pleistocene provoked drastic changes in the vegetation and the fauna (Tzedakis and Bennett 1995). During the interglacial periods, deciduous trees such as oak and lime-tree, were present, while during glacial periods steppe or tundra would cove much of the territory that Neanderthals inhabited (Sear 1935). The same changes can be observed for the fauna, where mammoth or woolly rhinoceros persisted during the cold periods, and fallow deer and great horned owls lived in a forested environment compatible with an interglacial temperature (Wicander and Monroe 2007). The number of plants that Neanderthals could consume would drop drastically during the glaciations, thus forcing them to eat more meat. However, even this food would be rare, because the herbivores would migrate. This in turn forced the Neanderthal migrate into more hospitable regions. In coastal areas, such as Gibraltar, there is evidence that, in addition to large animals, Neanderthals would hunt small mammals and birds and consume marine resources such as mollusks, shellfish, tortoises, and fish (Toussaint et al. 2011; Patou-Mathis 2012).

During OIS 3 the weather cycles fluctuated more rapidly (in a matter of decades) between extreme cold and more mild conditions. Neanderthal bodies were physically well suited for survival in cold climates, but during OIS 3, plants and animals would be replaced by completely different ones within a single, Neanderthal's lifetime. For instance, a forest would change into a tundra (Balin et al. 2012; Won 2012). This has been hypothesized to have been a possible reason for the extinction of Neanderthals, which disappear from Europe between 40,000 and 30,000 years ago (Condemi 2001; Rosas A. et al. 2008). Neanderthal extinction is still not fully explained, as the reasons could be diverse. One way to evaluate this extinction could be to understand Neanderthal evolution.

In 1997, Krings et al. (1997) successfully sequenced mitochondrial DNA (mtDNA) from a Neanderthal specimen from Feldhofer cave in the Neander Valley. Since then the DNA from nineteen Neanderthals has been sequenced. These Neanderthal specimens came from Spain: El Sidron and Valdegoba (Torres de T et al. 2010); France (La Chapelle-aux-Saints and Les Rochers-de-Villeneuve); Belgium (Engis and Scladina); Germany (Neanderthal); Croatia (Vindija) and Italy: Saccopastore (Sergi 1948; Condemi et al. 2013). In order to understand the demographic structure and evolution, and geographic distribution of the Neanderthals, Fabre et al. (2009) used these DNA databases to model different scenarios of Neanderthal evolution. After each simulation, measures of genetic diversity were calculated, and the authors evaluated the adequacy of fit for each model. Their results suggest that there were at least three, genetically distinct, Neanderthal populations: one in western Europe (west), one in the southern Europe and the Middle East (south), and one in the western Asia (east).

Whereas Fabre et al. (2009) seek to evaluate the existence of molecular indicators of population-level differences among the Neanderthals, the goal of this study is to evaluate variation in morphological characters of the Neanderthal dentition. If dental characters do show variation then I seek to determine whether Neanderthal teeth vary over time and/or across space, thus providing evidence of micro-evolutionary change within this species. An evolutionary change in the Neanderthal dentition though time will be used to evaluate species-level changes over a 250,000 year period. Geographic variation will be used to evaluate whether dental data can be used to recognize geographically-defined, Neanderthal populations and which, if any, previous hypotheses about Neanderthal subgroups are supported by dental data. In addition, spatial distribution of dental characteristics will allow me to evaluate population movement patterns. To evaluate these questions, I will perform statistical analyses of Neanderthal dental characters on representative specimens from several Neanderthal sites across Europe. Samples will be evaluated both spatially and temporally to evaluate Neanderthal evolution across space and through time.

Figure 1. 2. Expansion of the Neanderthals sites from Portugal on the Atlantic coast at Lagar Velho to the Altai site in Siberia at the Denisovan Cave.

Chapter 2: Literature Review

History of the Neanderthal Problem

The cranial cap marked by a receding forehead and prominent browridges and accompanying remains found in August 1856 in the Neander Valley became a puzzle for paleontologists, because there were no comparable bones (Schaaffhausen 1868). Were they human remains? Different hypotheses were proposed, including that they were remains of a Mongol soldier of the Russian army marching in France in 1814 or human fossils dating to the so called "pre-diluvian animals." A respected German medical doctor and anthropologist, Rudolf Virchow, examined the original fossil and his report to the Berliner Gesellschaft für Anthropologie, Ethnologie und Urgeschichte, indicated that the Neanderthal was an abnormal human being, probably deformed, and dead of arthritics and rickets (Buikstra et Robert 2012). This last idea was still defended in 1970 by Francis Ivanhoe (1970) of the University of London. In the years following, the first recognized Neanderthal discovery, an increased in the number of Neanderthal fossils confirmed the species status of *Homo neanderthalensis* (King 1864).

A turning point in the study of Neanderthals occurred in 1908, when two young researchers recovered a buried Neanderthal skeleton in the small French village of La Chapelle-aux-Saints. Professor Marcellin Boule of the National Museum of Natural History of Paris was in charge of the study (Boule 1912). As a result of his investigation, he underlined the similarities between modern humans and Neanderthals. However, with their more archaic features, Neanderthals were described as primitive brutes without moral or aesthetic preoccupation. Boule ignored completely the fact that this fossil was discovered in a burial, and preferred to emphasize another cultural aspect of Neanderthals: the presence of cannibalistic practices, well shown on the Croatian Krapina Neandertals published by Gorganovic-Kramberger in 1906.

It wasn't until later, that intentional burials among Neanderthals were confirmed by discoveries at La Quina (Henri-Martin 1923; Verna et al. 2012) and at La Ferrassie (Heim 1976) in France as well as at Shanidar, Iraq (Solecki 1957; Trinkaus 1993). Cannibalistic activities also have been confirmed in many Neanderthals sites including Marillac (Mussini 2011) and Abri Moula, France (Defleur et al. 1999), El Sidron, Spain (Rosas et al. 2006) and Goyet, Belgium (Rougier et al. 2016) where even human bone tools were produced. Thus, it should be noted that the practice of cannibalism is known from the OIS 5 (130,000 to 74,000 years ago) at Abri Moula in France and at Krapina in Croatia, and during the time that burials associated with Neandertals are known, during the OIS 4 (74,000-59,000 years ago) at Marillac-les Pradelles in France, at El Sidron in Spain and during the OIS 3 (40,500 years ago) in Goyet in Belgium. We don't know the significance of the cannibalism. Some authors (Carbonell et al. 2010) have considered it as an aspect of their economic system, whereas others consider it to have been a mortuary practice (Tillier 2013). It is almost impossible to know if cannibalism occurred only between external groups (clans) or if it was also practiced within groups (Condemi 2016).

Studies of the Origins of Neanderthals

The origin and the evolution of the Neanderthal have been studied for a long time (Schaaffhausen 1868; Fraipont and Lohest 1886; Boule, 1912; Duckworth1912; Elliot Smith 1928; Bar Yosef and Vandermeersch 1991; Mallegni 1995; Mann and Vandermeersch 1997;

Rosas 2000; Quam et al. 2001; Voisin 2006; Harrold 2007; Richards et al. 2007;Lumley (de) 2009; Martinon-Torres et al. 2008; Nowaczewska et al. 2013; Semal et al. 2009; Vandermeersch and Garralda 2011; Churchill 2014; Quam et al. 2015). In 1907, a mandible was extracted from a quarry near the village of Mauer, a few kilometers from Heidelberg, Germany (Schmitz et al. 2002). Except for the premolars and the first two left molars, the mandible was nearly complete. The German scientist Shoetensack (1908) proposed the species name *Homo heidelbergensis.*

Since 1971, excavations directed by de Lumey at the site of Tautavel, France have unearthed the remains of several *Homo heidelbergensis* specimens, including a skull with an age estimation of 450,000 years ago. The site of Sima dello Huesos in Atapuerca, Spain has also produced several *H. heidelbergensis* specimens (Arsuaga et al. 1997a). These fossils indicate that the Neanderthal characters evolved at different rates as a series of adaptations, due to the environmental pressure, and influenced the evolution of different parts of the anatomy (Lalueza-Fox and Sanchez-Quinto 2015). For example, the Arago, *H. heidelbergensis*, skull possesses Neanderthal characters such as a prognathism of the facial region and the obliquely receding malar bone (Condemi 2016). These features are more developed on Neanderthal skulls and suggest that Neanderthal features begin appearing in *H. heidelbergensis* roughly 450,000 ago Meyer et al. (2016) indicates that the analysis of the mitochondrial and nuclear DNA data from Sima de los Huesos suggests that the Neanderthal and Denisovans, an extinct early human found in Siberia, were closely related and that they probably split from the *H. heidelbergensis* about 500,000, while the *Homo sapiens* split about

650,000 years ago. Given the presence of Neanderthal characters, these fossils show that the differentiation of the European Neanderthal was already underway now.

As the analyses of OIS 5 fossils have demonstrated, the emergence of the Neanderthal population was not sudden but progressive (Condemi 1992). Over the course of time, fossils exhibit an increasing number of Neanderthal characters (Dean et al. 1998). The complete set of Neanderthal features are seen from OIS 5 to the disappearance of Neanderthals during OIS 3.

Variability and Diversity

Neanderthals have been discovered in a vast geographical area that extends from Portugal to Uzbekistan and from northern Europe to the Middle East. Moreover, most Neanderthal sites in Europe have yielded only very few human remains. It has been estimated that until the present only about 300 individuals of this population have been recovered in Europe (Condemi 2016). Whereas complete Neanderthal skeletons are known, the majority of specimens consist of teeth and highly fragmented parts of the cranium and post-cranial skeleton. These remains are what is left for anatomical studies of the humans who peopled Europe during the Middle and early Upper Pleistocene.

If paleoanthropologists agree in their observation of the difference between European and Middle Eastern Neanderthals (Vandermeersch 1981; Condemi 1988; Stefan et Trinkaus 1998; Condemi 1992; Churchill 2014), the interpretation of these differences among the Neanderthals is still subject of discussion. What makes the interpretation difficult and complex, is that the number of fossils is limited. This makes the identification of regional characters of the various Neanderthal groups uncertain. A corollary point is that the

Neanderthals are present in a large geographical area with a great diversity of climatic conditions. This raises the question concerning the degree of regional homogeneity, where minor diversity observed between Neanderthal individuals is often attributed to individual variation or to sexual differences. From a paleoanthropological point of view, one might wonder whether it might not be possible, in such a large region, to identify groups corresponding to distinct geographical localities or to see a chronological diversity though time from OIS 5 to OIS 3.

From analyses of the post cranial bones, notably the upper limbs, Voisin (2004, 2006) indicates that numerous characters of the Neanderthal exhibit a geographical gradient. Clavicle morphology of Near Eastern Neanderthals is different from that of Western European Neanderthals. Anatomical variation on the clavicle shape shows that all western Europe Neanderthal scapulae have a dorsal *axillary sulcus*, but in Central Europe and the Near East the *sulcus* can be dorsal or bisulcate (Frayer 1992). Based on humeral morphology Hambücken (1993, 1997) distinguished two main groups of Neanderthals, a western European Neanderthal (from Spain, France and Belgium) and a Middle Eastern Neanderthal (from Central and eastern European Neanderthals) and attributed their differences to their evolving in different environments. The Western European Neanderthal was further divided into “Classic” Neanderthals, which included specimens from western France, Germany, and Belgium and a Mediterranean group, consisting of specimens from southern France, Spain and Croatia (Sergi 1948; Lumey (de) 1978; Giacobini and Lumey (de) 1984; Maureille and Houet 2005).

Based on mitochondrial DNA variability, Fabre et al. (2009) have defined three subgroups, of “classic Neanderthal,” a Western subgroup (Figure 2.1) from the North of Spain through Slovakia, a Southern subgroup that includes the south of Spain, Italy, Croatia and Greece (Figure 2.2), and an Eastern subgroup (Figure 2.3) that extends from the Caspian Sea through Russia. Voisin (2012) notes that the Neanderthals, being neither morphologically nor genetically homogenous, vary in trait expression from east to west. The western Neanderthal were described as “Hyperneanderthals,” exhibiting the full suite of “classic Neanderthal” characteristics, while the Near East Neanderthals were “Hyponeanderthals,” displaying fewer of these characteristics.

Neanderthal Size Population and Genetic Variations

In 1991, a Neanderthal specimen recovered near Düsseldorf, Germany in 1856 was the subject of an interdisciplinary project in which mtDNA was extracted for analysis. The resulting mtDNA genome was published by Krings et al. (1997). This initial study was followed by mtDNA studies of others Neanderthal fossils, including Mesmaïskaya, Russia and Vindija, Croatia in 2000, Engis, Belgium, La Chapelle aux Saints, France, les Rochers de Villeneuve, France in 2004, El Sidron, Spain in 2005, 2006 and 2011(Rosas et al. 2011), Monti Lessini, Italy and Scladina, Belgium in 2006, Teshik-Task, Uzbekistan and Ikladnivok, Russia in 2007 and Valdegoba, Spain in 2012 (Ovchinnikov et al. 2000; Scholz et al. 2000; Caramelli et al. 2003; Serre et al. 2004; Lalueza-Fox et al. 2015; Orlando et al. 2005; Krauze et al. 2007; Dalen et al. 2012). These studies suggested a low diversity of the mtDNA and underlined the existence of an east-west genetic divergence. Evidence of this divergence can be seen in the low mtDNA variation among recent western European Neanderthals (less than

50,000 years old) compared to Eastern and older European Neanderthals. The presence of mtDNA diversity in the OIS 5 (Orlando et al. 2007) indicates also that Neanderthal endured a bottleneck that has been revealed around 60,000 years ago (Sanchez-Quinto and Lalueza-Fox 2015) during the cold OIS 4.

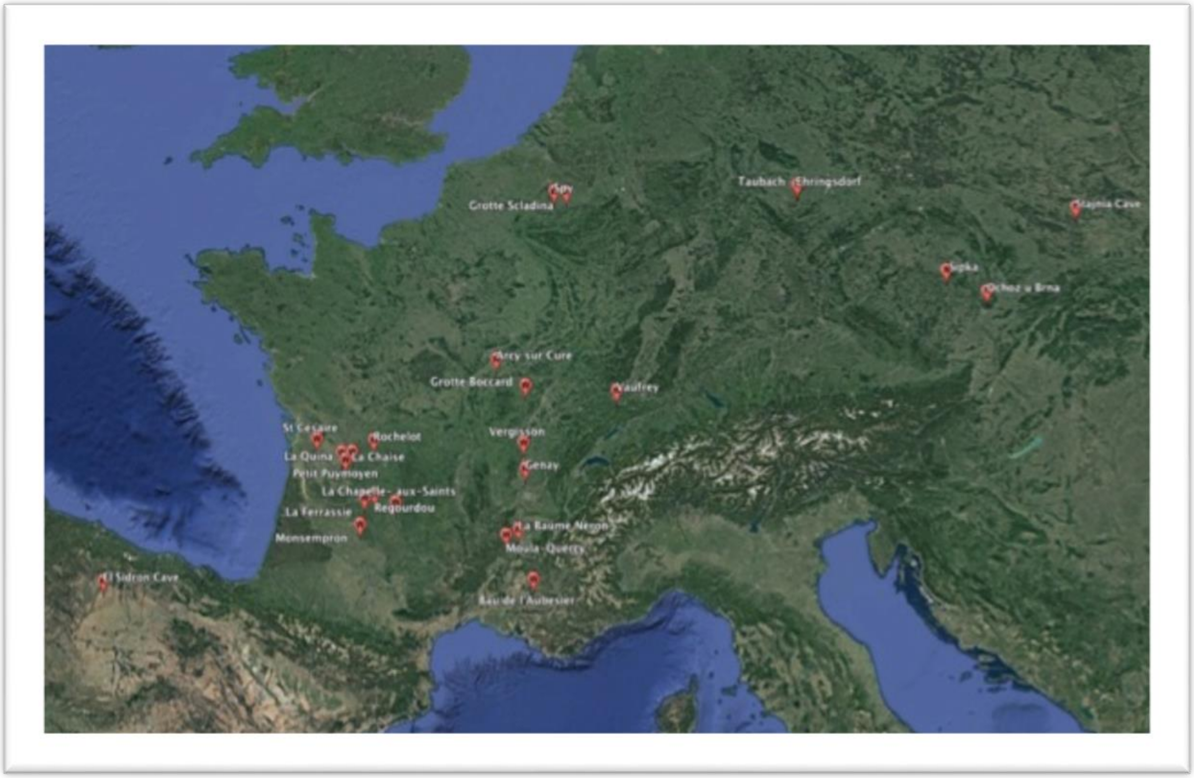


Figure 2.1. Sites of the “classical” Neanderthal in western (France, Belgium) and northern Europe (Germany, Czech, Poland).

Figure 2.2. Sites of the “classical” Neanderthal in southern region Spain, Croatia, Italy, Greece, Israel, Iraq, Uzbekistan.

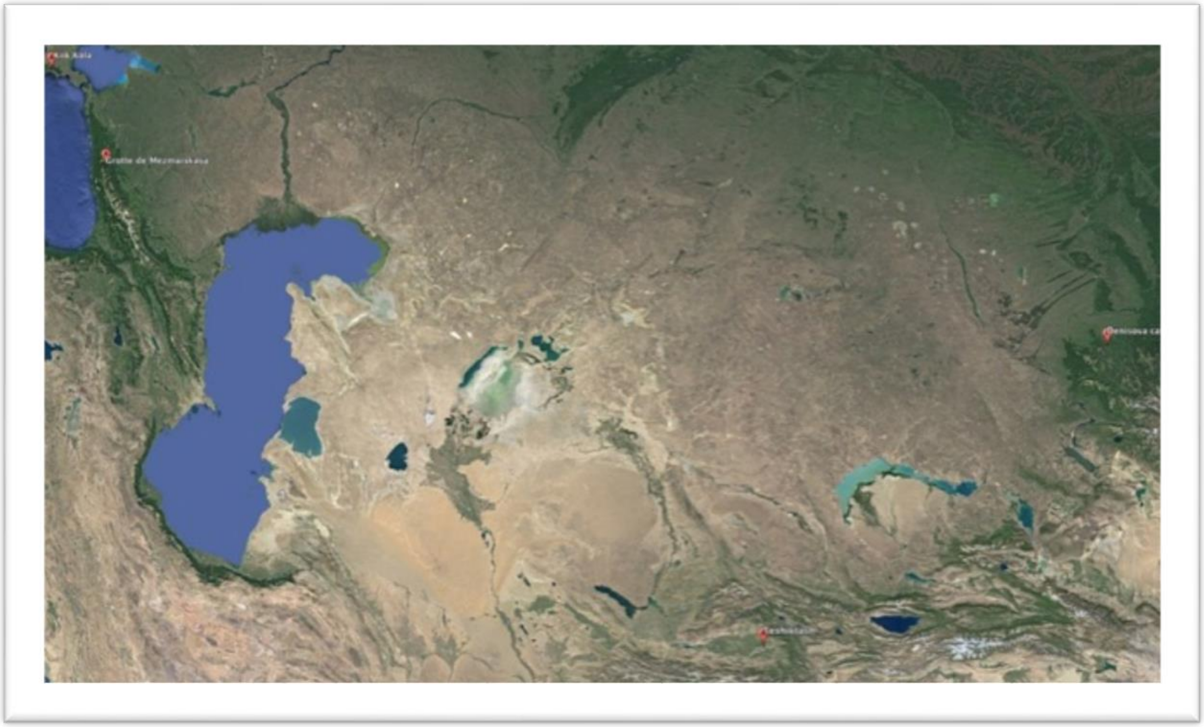


Figure 2.3. Sites of the “classical” Neanderthal in Eastern Europe and Siberia (Russia).

Results of mtDNA studies reveal an east –west morphological cline among Neanderthals consistent with isolation by distance (Voisi 2012; Ovchinnikov et al. 2000; Scholz et al. 2000; Caramelli et al. 2003; Serre et al. 2004; Lalueza-Fox et al. 2015; Orlando et al. 2005; Krauze et al. 2007; Dalen et al. 2013). For these studies, the Neanderthal mtDNA sequenced were similar to each other, underlining a general low diversity (Lalueza-fox et al. 2015). Sanchez-Quinto and Lalueza-Fox (2015) contend that a combination of different factors, such as inbreeding, population size, and the accumulation of deleterious genes may have led to Neanderthal extinction. On this last point, Condemi (2016) points out that the Neanderthals occupied an immense territory and probably had little contact with other clans, thus, increased inbreeding and the accumulation of genetic mutations would reduce life expectancy. Orlando et al. (2007) report that the short sequence of mtDNA extracted from the 100,000-year-old molar of a child from Scladina, Belgium disclosed the genetic depletion of the Neanderthal.

Analysis of Dental Remains

There are several advantages to using dental characters in population studies. First of all, dental size and shape appear to be under genetic control (Scott and Turner 1988; Smith 1991), and this permits the use of dental components to trace back heritability. Heritability can be defined narrowly as the ratio of the genic variance for a characteristic to the total phenotypic variance for that population. In the broad sense, it is the fraction of the total variance that is attributable to differences among the genotypes (Wilson 1982). Second, because of their resistance to deterioration, teeth are the best preserved biological remains, and are thus more readily available. Third, teeth vary within and between populations (Scott 2008). Thus, they can be used to compare the populations. Finally, teeth register a great number of life history events, such as development, diet, and stress. Dental morphology analysis is a good method to examine intra-population variation, inter-population relationships, gene flow, and microevolution (Heather 2009). The genetic control makes tooth morphology less dependent on external factors and data gathered from the teeth are easy to compare with others across space and time. This makes it easier to track gene flow (Heather 2009).

Alt and Turp (1998) have presented an entire catalog of dental anomalies suitable for modern inter-population analysis. Teeth can include additional cusps or roots. They also may have an abnormal position or malocclusion. In general, these rare anomalies are useful, because their common presence in different populations indicates a gene flow between them. These phenotypic data are good sources of information to estimate differences or similarities among regional or continental populations (Stojanowski and Schillacci 2006).

Odontological characters have been used to investigate evolutionary processes (Johnson and Lovell 1994) or diachronic changes in character expressions in a region (Lukacs and Hemphill 1991; Cucina et al. 1999; Gravere 1999; Coppa et al. 2007). The first anthropological application of dental characters to evaluate Neanderthals focused mainly on metric data to describe and classify Neanderthals (e.g., Boule 1912; Patte 1955). These studies focused primarily on cranial and post-cranial skeletal anatomy (Hublin 1978; Rosenberg 1988; Trinkaus 1988) and utilized the dentition to evaluate tooth size and dental reduction during the later Pleistocene (Wolpoff 1978; Brace et al. 1987; Bailey 2006).

One approach for analyzing Neanderthal teeth is metric analysis, based on measurements of different features. Metric approaches are adequate to study the variability in population where subgroups can differ in details of size and shape. Wolpoff (1978) used metric features to determine wear rates among Neanderthal. Bermudez de Castro et al. (2003) used dental metrics to study the rates of anterior tooth wear of the Sima de los Huesos dental remains. Bailey and Hublin (2006) made a metric comparison of the permanent teeth of the Grotte du Renne (Bailey and Hublin 2008) Neanderthal with those of contemporary modern humans by comparing buccolingual tooth breadths. Condemi et al. (2010) used metrics to compare the Neanderthal dental assemblage of the Rhone Valley corridor with those of other Neanderthal data using two linear measurements and three indices (Condemi et al. 2010).

Non-metric observation is an approach that evaluates character frequencies based on the presence or absence of characteristics such as fissure patterns, accessory ridges, cusp and root numbers and degree of character development or form (e.g. curvature and angles) (Zubov 1973, 1979; Scott and Turner 1997; Hillson 2003; Stojanowski and Schillaci 2006). Non-metric morphological dental characters may result from micro-evolutionary forces of genetic admixture (Turner 1969; Pino-Cisternas et al. 1995; Khudaverdyan 2011b), mutation (Morris et al. 1978), genetic drift (Turner 1969; Postnikova 1974; Scott and Dahlberg 1982; Segada 1993; Zubova 2008, 2010; Khudaverdyan 2009; Vargiu et al. 2009), and/or natural selection (Dahlberg 1963; Scott and Turner 1988). From this point of view, dental characters are largely controlled by genetics, and they are free of sex and age bias (Scott and Turner 1997; Hillson 2002). Non-metric dental character analysis can be used to assess biological relationships between populations (Bailey 2006a; Khudaverdyan 2013) and to trace evolutionary change arising from changing settlement patterns (Khudaverdyan 2013). The problem with non-metric characters is the risk of introducing undesirable errors that may arise due to subjectivity in scoring procedures. Character frequencies may be biased due to poor preservation as well as due to the division of continuous features into discrete characters (Hauser and DeStefano 1989). Observation errors may also arise due to unclear phenotypic features

The consensus, based on molecular data, is there are at least three main Neanderthal regions, corresponding to an east-west cline. These regions are reported as a Near East, a Central and a West Europe region (Hambücken 1993, 1997; Krings et al. 1997; Daten et al. 2011; Fabre et al. 2009). This consensus surrounding Neanderthal distribution and evolutionary patterns raises several important issues surrounding the relationship between Neanderthal dental morphology and population structure. These issues include whether dental characters can be used to identify Neanderthal subgroups and, if so, whether these subgroups correspond with those proposed by Fabre et al. (2009). Questions also persist regarding whether dental data might allow us to evaluate Neanderthal population movement patterns and temporal trends in Neanderthal dental evolution. This study seeks to addresses these issues through an analysis of Neanderthal dental variation.

Chapter 3: Method and Materials

Method

Biodistance is a statistical measure of observable phenotypic similarities that are related to genotypic similarities, potentially identifying biological affinity between individuals (Pilloud and Larsen 2011). In other words, it is the measurement of biological relatedness (or divergence) between and within populations. The major premise of biodistance analysis is that variation in phenotypic characters reflects genetic variability (Stojanowski and Schillacci 2006; Hubbard et al. 2012). For instance, biodistance analyses use phenotypic data from the dentition to estimate genetic similarity among regional or continental populations to reconstruct patterns of gene flow, population origins, or long-distance migration (Buikstra et al. 1990; Larsen 1997; Sutter and Mertz 2004; Irish 2005; Matsumura and Hudson 2005; Stojanowski and Schillacci 2006). The slow rate of tooth evolution (Turner et al. 1991; Irish 2005) is favorable for biodistance analyses. Dental phenotype consists of polygenic non-metric characters (Hauser and DeStefano 1989). Character frequencies will be the primary descriptive statistic (Stojanowski and Schillacci 2006).

For practical reasons, I used Condemi's classification of Neanderthal evolution, which is based on geological age and an increase of the number of Neanderthal characters. The first three stages of Neanderthal evolution can be classified as pre-Neanderthal. These pre-Neanderthals differ from later Neanderthal stages in displaying fewer Neanderthal characteristics. The fourth stage of Neanderthal evolution is termed "Proto" Neanderthal and the fifth is referred to as "Classic" Neanderthal. These final two stages exhibit the full range of Neanderthal characteristics. Due to the gradual accumulation of Neanderthal traits through time, I will evaluate only samples from proto-Neanderthals and classic Neanderthals. This will allow me to avoid any misinterpretation concerning Neanderthal non-metric dental features. These final two stages of Neanderthalization correspond to a period stretching from 130,000 to 35,000 years ago (OIS 5-3) (Condemi 2001).

Neanderthal teeth are known for the high frequency of certain features (Patte 1955; Bailey and Turner 1999; Bailey 2001, 2006; Hillson 2002; Bailey 2002, 2005; Bailey et al. 2010), and the dental characters evaluated here were selected due to their practicality for the research. They are easy to observe and to identify, have a clear genetic component and have a high record of replicability. Characters were also selected due to their successful use in previous studies. For instance, researchers have successfully used dental characters, such as the number of molar cusps or the fissure patterns, to describe and differentiate modern human populations from different world regions including Asia, Australia, Africa and the Americas (Dahlberg 1963; Hanihara 1967; Scott et al. 1983; Turner 1992; Irish 1993). These characters allow us to compare the results over the same subject such as the number of cusps (Irish 2005).

In addition to specimens obtained from the published literature, I evaluated specimens housed at the National Museum of Natural History of Paris, as well as specimens provided by Professor Condemi. Data were collected from digitized specimens of Krapina, obtained from the Croatian Natural History Museum, Zagreb. I acquired published data available through the NESPOS and the website anthropologicaldata.free.fr database.

To evaluate biodistance between potential Neanderthal populations, characters were scored as present (1) or absent (0) for each specimen. If a character could not be scored due to the quality of the specimen or heavy wear, no score was given. Data for each character at each site were summarized in a matrix of relative frequencies (number of teeth for which the character is present/total number of teeth evaluated). In total, 487 specimens were scored from 52 sites across Europe and the near East. These specimens consisted of 244 molars, 115 premolars, 57 canines and 71 incisors. A total of 68 characters were scored. Specimens, sites, and the OIS periods are presented in the appendix.

Characters.

Incisor characters (Figure 3.1)

Character 1: I^1 Labial Convexity

Character 2: I^2 Labial Convexity

Character 3: I_1 Labial Convexity

Character 4: I_2 Labial Convexity

Convexity refers to the curve on the labial surface when observed from the occlusal view (Hillson 2003). Bailey (2001, 2006) has signaled that incisor convexity occurs in high frequencies among Neanderthals.

Character 5: I^1 Shoveling

Character 6: I^2 Shoveling

Character 7: I_1 Shoveling

Character 8: I_2 Shoveling

Incisor shoveling occurs when well-developed marginal ridges form on the mesial and distal borders of the lingual incisor surface. These ridges enclose a deep fossa and can be observed from the lingual and incisal aspects of the tooth crown (Hillson 2003). Maureille et al. (2008) indicate shoveling in a lateral incisor found in the Boccard cave.

Character 9: I^1 Lingual tubercle

Character 10: I^2 Lingual tubercle

Character 11: I_1 Lingual tubercle

Character 12: I_2 Lingual tubercle

The lingual tubercle can be observed on the lingual side of both upper and lower incisors. It consists of a broad ridge of enamel that extends occlusally from the cervical margin of the tooth crown, and it ranges in form from one or more ridges to a cusp with a free apex. Toussaint and Bonjean (2014) indicates that the combination of marginal ridges (shoveling), labial convexity, and lingual tubercle may be used to distinguish Neanderthal incisors. Bailey and Hublin (2006) corroborate this finding.

Character 13: I^1 Interruption groove

Character 14: I^2 Interruption groove

Character 15: I_1 Interruption groove

Character 16: I_2 Interruption groove

An interruption groove, is a fissure found on the lingual surface of the incisor crown that crosses the cingulum, often reaching the root. Whereas is can occur in one or more of three alternative positions (mesial, distal or medial), the position of this feature is not considered in scoring the character as present or absent. This character can be observed from the lingual side of the tooth. Toussaint and Bonjean (2014) describe also the presence of two "interruption grooves" that cut the tubercle from the distal and mesial marginal ridges.

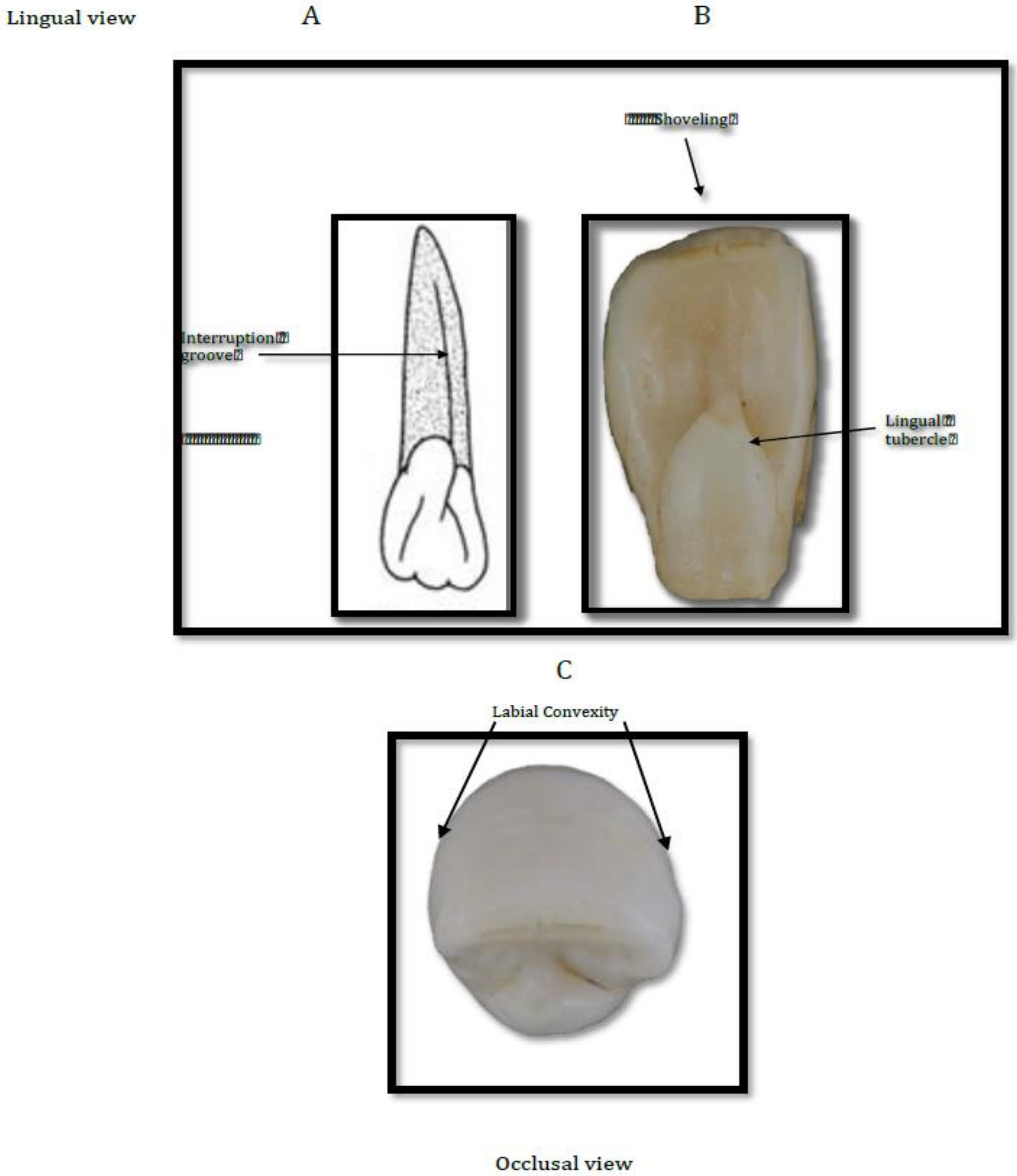


Figure 3.1. Upper incisor characters: A) Line drawing of left I^2 in lingual view showing the presence of the interruption groove. B and C) left I^2 from Krapina (Croatia) in lingual (B) and Occlusal (C) views showing the presence of shoveling, the lingual tubercle, and labial convexity. In A, mesial is to the right. In B and C mesial is to the left. (Modified from the Croatian Natural History Museum, by Luka Mjeda and Hillson 2003).

Canine characters (Figure 3.2)

Character 17: C^1 distal accessory ridge

Character 18: C_1 distal accessory ridge

As defined by Hillson (2003) the “distal accessory ridge” is outlined by a groove separating the central and distal crown elements on the lingual side. This is to be observed from the lingual view. Bailey (2006) indicates that the distal accessory ridge is 66.7% more common in Neanderthals versus early modern *Homo sapiens.*

Character 19: C^1 Mesial ridge

Character 20: C_1 Mesial ridge

The mesiolingual ridge is larger than the distolingual ridge. It intersects the lingual tubercle without being separated from it by a groove (Hillson 2003). Bailey (2006) notes the absence of this character in early Afro-Asians. This trait reaches a relative frequency of 14.3% in early modern Europeans, while the Neanderthals reach a relative frequency of 42.9%.

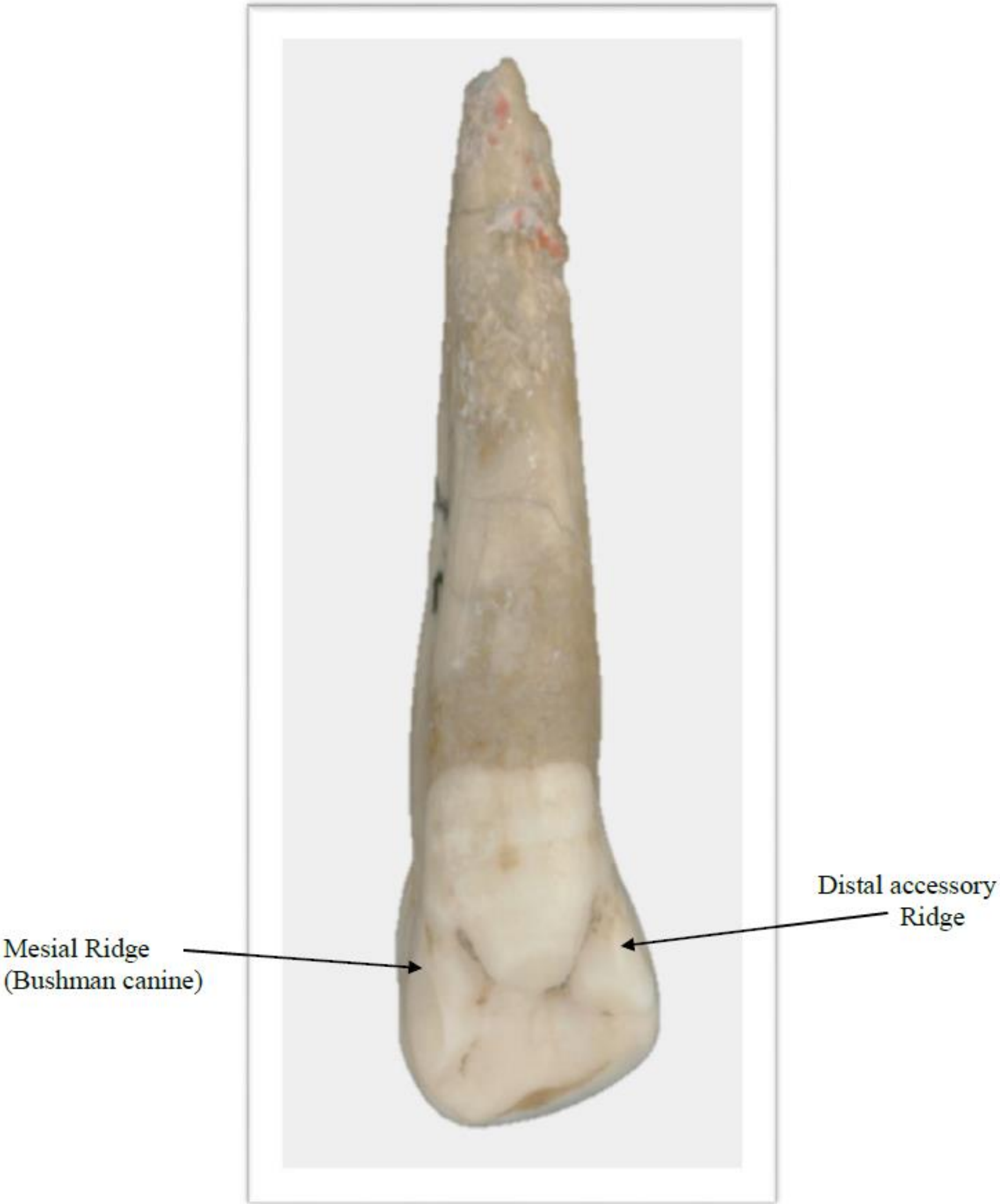


Figure 3.2. Right C^1 lingual view from Krapina (Croatia) (Modified from Croatian Natural History Museum, by Luka Mjeda).

Premolars characters.

Upper premolar P^3, P^4 (Figure 3.3)

Character 21: P^3 Bifurcation essential crest buccal/ lingual.

Character 22: P^4 Bifurcation essential crest buccal/ lingual.

The essential crest is present in almost every specimen and is often bifurcated in form (58% P^3 and 70% P^4) (Bailey 2006).

Character 21: P^3 Accessory ridge mesial/distal

Character 22: P^4 Accessory ridge mesial/distal

Mesial and distal accessory ridges are frequent (63% P^3 and 70% P^4), more often on the buccal side (Bailey 2006).

Character 23: P^3 Accessory cusp mesial/distal

Character 24: P^4 Accessory cusp mesial/distal

P^3 and P^4 have a similar morphology with mesial and distal accessory cusps (67% P^3 and 48% P^4), more frequently distal than mesial (Bailey 2006).

Lower premolars P_3, P_4 (Figures 3.4, 3.5, 3.6, 3.7)

Character 25: P_3 Mesiolingual groove

Character 26: P_4 Mesiolingual groove

The mesiolingual marginal ridge is interrupt by a groove extending from the fossa. This groove is often present among the P_3 crown. It has a higher frequency of the mesial lingual groove than in modern human (Bailey 2006).

Character 27: P_3 Transverse crest

Character 28: P_4 Transverse crest

P_3 and P_4 show a strong and continuous transverse crest connecting the protoconid and metaconid (77%). The combination of a marked transverse crest with asymmetrical outline and multiple lingual cusps (61% of Neanderthals) distinguish Neanderthals (Bailey, 2006).

Character 29: P_3 distal accessory ridge

Character 30: P_4 distal accessory ridge

Neanderthal higher frequency of the distal accessory ridge: distal with 90% and mesial with 24%, than in modern human (Bailey 2006).

Character 31: P_3 lingual accessory ridge

Character 32: P_4 lingual accessory ridge

This premolar has a low frequency (20%) of accessory lingual cusp (20%) (Bailey 2006).

Character 33: P_3 lingual accessory cusp

Character 34: P_4 lingual accessory cusp

In P_4 accessory lingual cusp has a high frequency (91%), which may take the form of single (40%) or multiple (50%) distolingual cusps (Bailey 2006).

Character 35: P_4 "U" fissure pattern

Character 36: P_4 "H" fissure pattern

Character 37: P_4 "Y" fissure pattern

The contact of the central, the two triangular, and the secondary grooves of the buccal cusp define the second “U” form. The “H” type has the central groove crosses the occlusal crown between the mesial and the distal pits, which gives the tooth a “H” form. The type “Y” is characterized by the contact between the lingual and the central groove. There is no transverse ridge. Wood and Uytterschaut (1986), point out that the fissure pattern of the premolars P_3 and P_4 shows evidence of affinities with different hominid categories (australopithecine). For these authors, P_4 gives a better distinction more and they suggest that details study of these teeth is useful for taxonomic diagnosis.

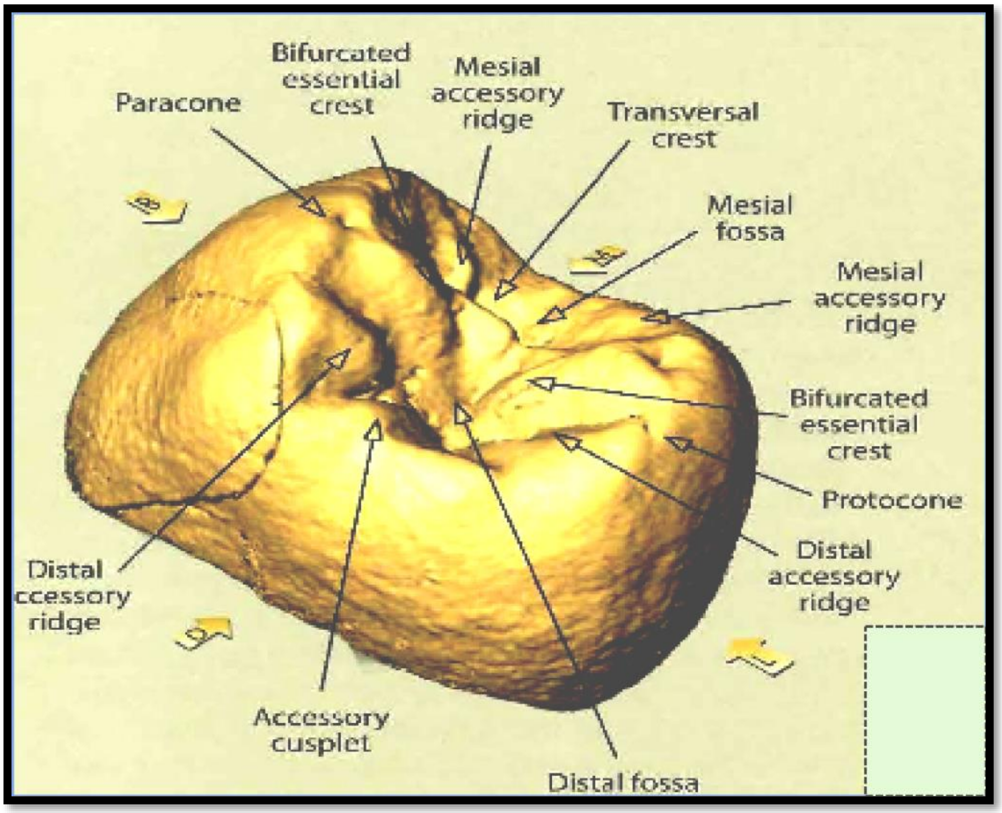


Figure 3.3. Right P^4 from Scladina (Belgium) (modified from Toussaint 2014).

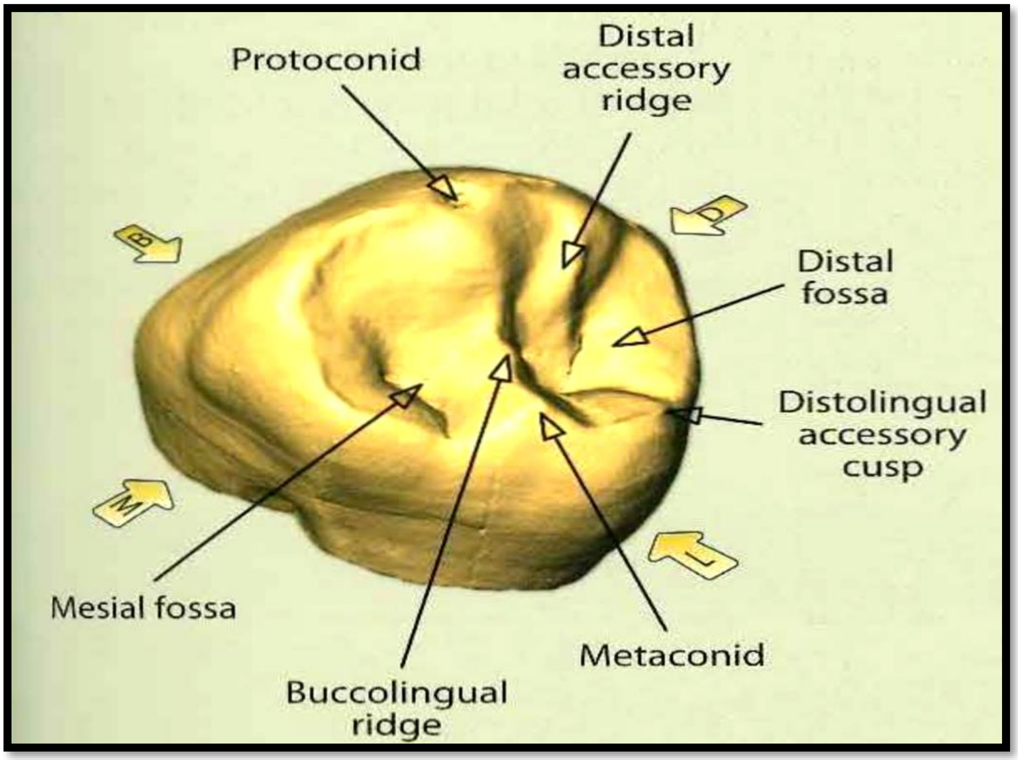


Figure 3.4. Right P_3 from Scladina (Belgium) (modified from Toussaint 2014).

Figure 3.5. Left P_4 “U” fissure pattern from Krapina (Croatia) (modified from the Croatian Natural History Museum).

Figure 3.6. Right P_4 “H” fissure pattern from Krapina (Croatia) (modified from the Croatian Natural History Museum).

Figure 3.7. Right P_4 “Y” fissure pattern from Krapina (Croatia) (modified from the Croatian Natural History Museum).

Molar characters.

Upper Molars (Figure 3.8)

Character 38: M^1 Cusp 4

Character 39: M^2 Cusp 4

Character 40: M^3 Cusp 4

Cusp 4 is in fact a late evolutionary addition and is the distolingual cusp of the upper molars (Scott 2008; Hillson 2003). Higgins (2009), underlines that Cusp 4 has the biggest variation in size of all the upper maxillary molar cusps. The genetic component is strong.

Character 41: M^1 Cusp 5

Character 42: M^2 Cusp 5

Character 43: M^3 Cusp 5

On distal marginal ridge between the metacone and the hypocone. It can wear down quickly, which make observations difficult for older adults (Hillson 2003; Scott 2008).

Character 44: M^1 Carabelli

Character 45: M^2 Carabelli

Character 46: M^3 Carabelli

It ranges in size from a slight deflected developmental groove to a large free-standing cusp that is almost the size of the hypocone (Hillson 2003; Scott 2008).

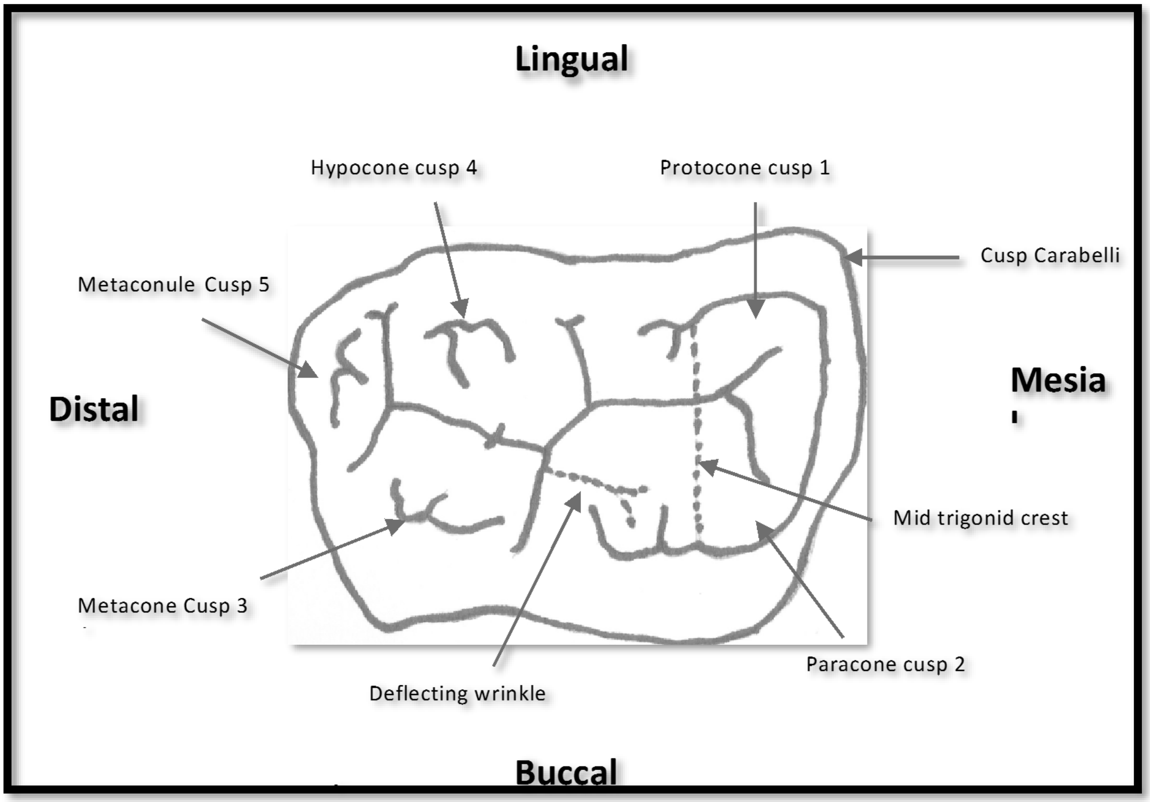


Figure 3.8. Upper molar.

Lower Molars (Figures 3.9, 3.10, 3.11, 3.12)

Character 47: M_1 Cusp 6

Character 48: M_2 Cusp 6

Character 49: M_3 Cusp 6

Cusp 6 (on distal marginal ridge) is an extra cusp, which appears between the entoconid and hypoconulid in the permanent mandibular molars. Difference of carriers and non-carriers of this character is quite easy, so that the teeth with this cusp can be simply counted as carriers regardless of size (Hanihara 1976; Hillson 2003).

Character 50: M_1 Cusp 7

Character 51: M_2 Cusp 7

Character 52: M_3 Cusp 7

These are extra cusps, which are located at the marginal border between the metaconid (cusp 2) and the entoconid (cusp 4). Cusp 7 appears more often on M_1 (Hanihara 1976; Hillson 2003).

Character 53: M_1 deflecting wrinkle

Character 54: M_2 deflecting wrinkle

Character 55: M_3 deflecting wrinkle

Deflecting wrinkle is a distally deflected (not straight) medial ridge on Cusp 2. It is distinguished by a change in course of the essential ridge about half way along its total length. The deflecting wrinkle is one of the formation of the median ridge of the metaconid. The ridge, when the deflecting wrinkle appears, shows a stronger development in either its length or breadth and curves distally at the central part of the occlusal surface. The teeth with wrinkles with little deflection, will scored as absent, even if the median ridge is well-developed. It is unusual to see this character in M_2 and $M_{3.}$

Character 56: M_1 “X”

Character 57: M_1 “Y”

Character 58: M_1 “+”

Character 59: M_2 “X”

Character 60: M_2 “Y”

Character 61: M_2 “+”

Character 62: M_3 "X"

Character 63: M_3 "Y"

Character 64: M_3 "+"

In the lower molars, deep fissures or grooves separate the major cusps. Variation in fissure pattern reflects which of the five cusps contact each other (see Figure 3.11). During hominin evolution, this fissure pattern started changing, especially for M_2. In modern humans, it is common for Cusp 1 and 4 to come in contact. This is designated as the "X" fissure pattern. A "Y" fissure pattern occurs when Cusps 2 and 3 are in contact. Between these two fissure patterns, there is a third and less common alternative where all four cusps come in contact at a single point and is designed as "+" (Maclic and Kaic 2002; Hillson 2003).

Character 65: M_1 Mid trigonid crest

Character 66: M_2 Mid trigonid crest"

Character 67: M_3 Mid trigonid crest

The mid trigonid crest (MTC) refers to an enamel crest that runs from the buccal margin of the protoconid (cusp 1) to the lingual margin of the metaconid (cusp 2) in lower molars, thus dividing the trigonid basin into mesial and distal portions. (Turner et al. 1991; Scott and Turner 1997; Bailey 2002). The MTC is considered to be typical for *Homo neanderthalensis* (Bailey 2002b; Martinón-Torres 2014).

Character 68: M_2 Distal trigonid crest"

Like the mid trigonid crest, the distal trigonid crest is a ridge of enamel that connects the protoconid and metaconid. However, in the distal trigonid crest, the ridge of enamel runs from the distal-most margin of the protoconid to the distal-most margin of the metaconid, thus isolating the trigonid basin from the distal half of the tooth.

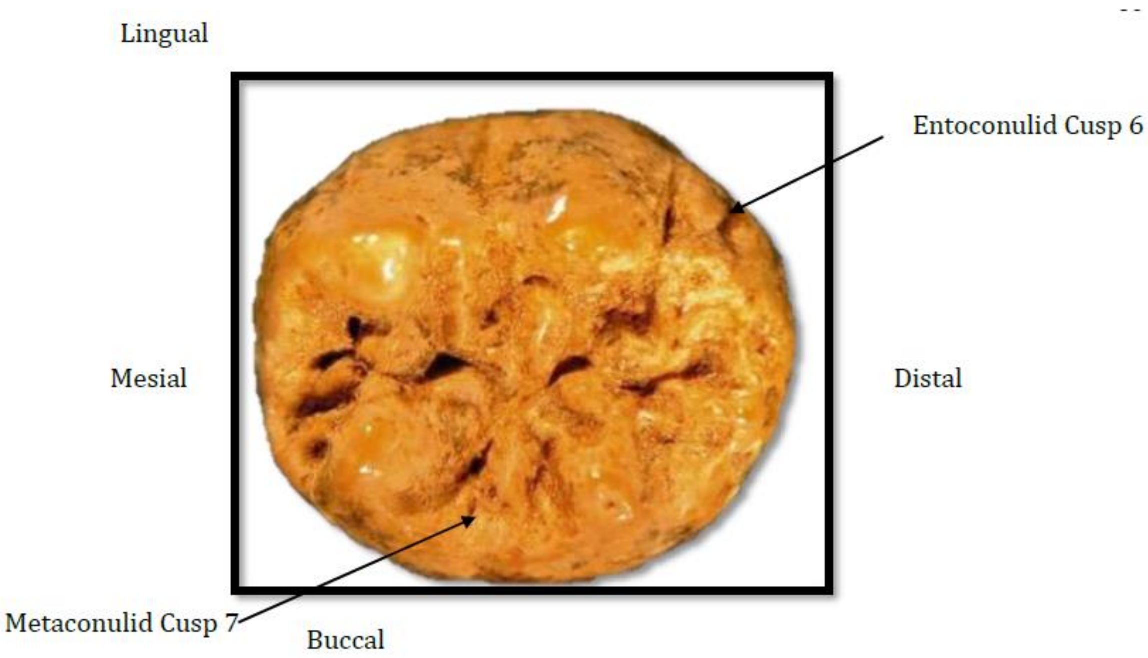


Figure. 3.9. Right M_1 with Cusp 6 and Cusp 7 (modified from Genay3, France. Document M. D. Garralda 2004).

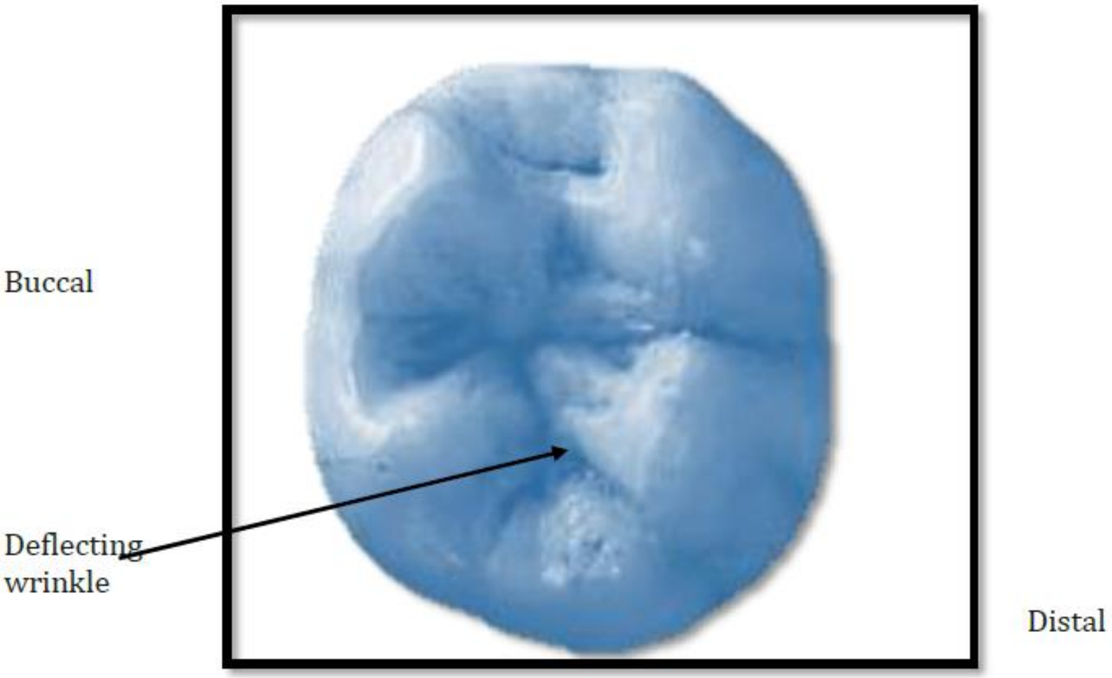


Figure 3.10. Right M_3 Deflecting wrinkle (Modified from Arcy-sur-Cure, France) (Bailey and Hublin 2006).

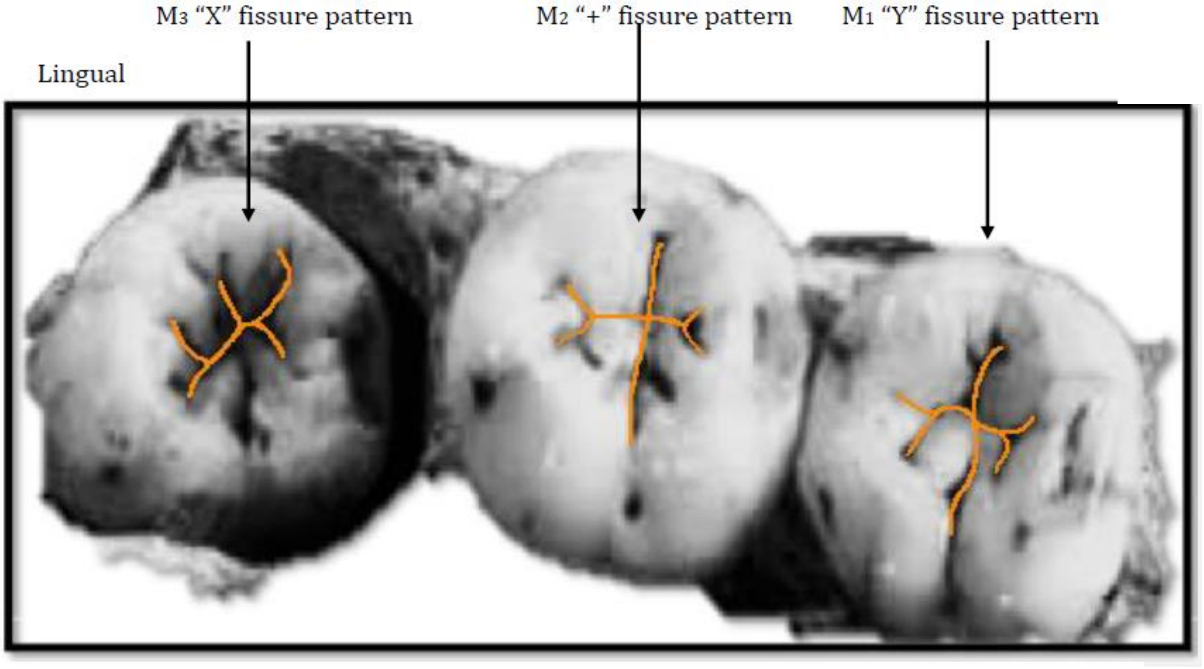


Figure 3.11. Right Molar fissure pattern. (modified Moulay–Guercy, France) (Hlusko l. et al. 2013).

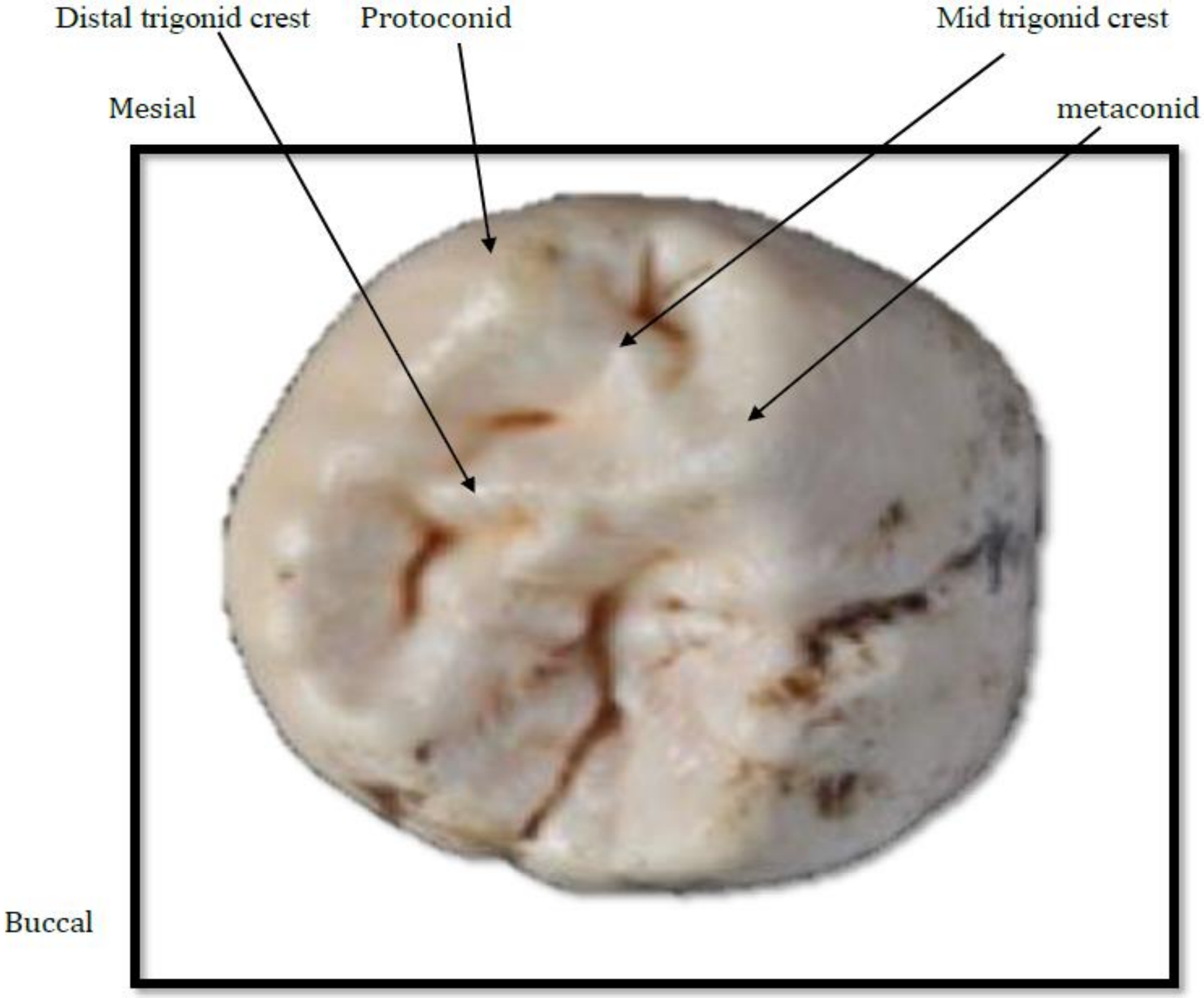


Figure 3.12. Mid trigonid crest (modified from Martinon-Torre et al. 2014).

Biodistance

Two approaches were applied to investigating biodistance between Neanderthal populations: a geographic approach and a chronological approach. The geographic approach involved grouping sites by region. Analyses were performed by country and by predefined regional sets. The country-level analysis involved treating specimens from sites within a politically defined country (e.g., France, or Croatia) as members of the same population. Broader, region-level analyses were performed on sites from broader, regions that may or may not conform to political boundaries. For example, regional analyses were used to evaluate biodistance between subgroups constructed by Fabre et al. (2009). Fabre et al.'s (2009) Wests subgroup extends from northern Spain to Denmark, and into western Russia. This subgroup includes the French sites of La Ferrassie, La Quina, Le Moustier, La Chapelle-aux-Saints, St. Cesaire, La Chaise (Bourgeois-Delaunay), Regourdou, Aubesier, the Spanish site of El Sidron, the German site of Ehringsdorf, and the Czech sites of Sipka and Kulna. The Southern subgroup consists of the western Spanish site of Zafaraya, the Italian site of Guattari, the Croatian sites of Krapina, and Vindija the Israeli sites of Amud, Kebara, and Tabun, and the Iraqi site of Shanidar (Rosas et al. 2008). Fabre et al.'s (2009) East subgroup runs from Central Asia to Siberia and includes site of Okladnikov in Siberia.

In the chronological approach, samples were grouped based on the age of the site from which they were recovered as indicated by oxygen isotopes (OIS periods). Isotopic stages considered here range from between 130,000 and 30,000 years ago. This time span is covered by three OIS periods: OIS 5 (warm), OIS 4 (Cold) and OIS 3 (warm). These are illustrated in Figure 3.13.

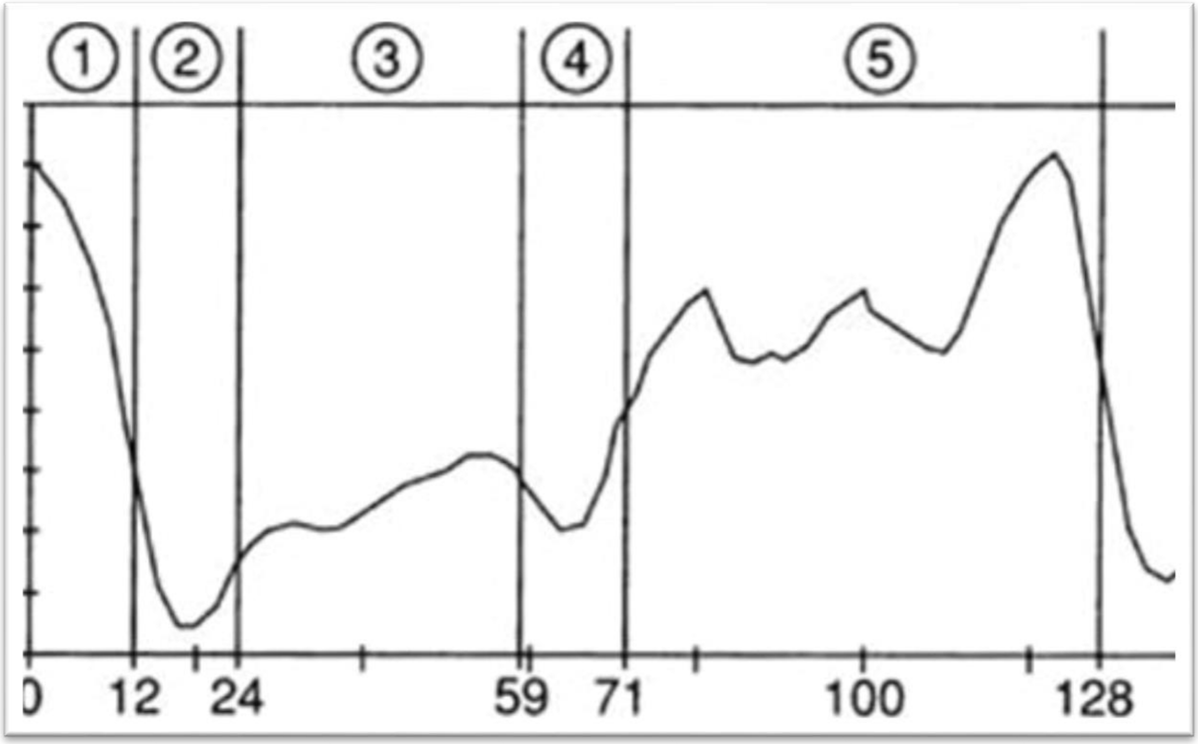


Figure 3.13. OIS periods from 128,000 years ago. Note the long period of OIS 5 and the brutal cold period of OIS 4 (modified from Shackleton and Opdike, 1973).

Statistical Analysis

To know, whether there are statistically significant differences in the means of the frequencies of characters (dependent variable) between samples from two geographic regions or OIS stages, I performed a series of independent 2 samples t-tests ($\alpha = 0.05$). Statistical analyses were performed using Minitab version 16.1.1 (2010). Whereas performing multiple t-tests is less than ideal, due to the very real chance of obtaining significant results simply due to the number of analyses performed, the structure of the data (e.g., missing data, partial data, etc.) precluded multivariate analysis. By performing a series of t-tests, I was able to increase my sample size for each character evaluated. Although methods for adjusting alpha levels when performing multiple-means comparisons have been proposed (Bonferroni 1936; Hochberg 1988), applying these methods proved unrealistic, given the large number of t-tests performed. Based on the results of the t-tests the number of characters used to investigate biodistance was reduced from the initial number of 68 scored characters to 38 (Figure 3.1) or fewer characters, depending on how many of these significantly variable characters could be scored for specimens from each geographic location. Differences between geographic regions were evaluated using Ward's method of hierarchical cluster analysis in the statistical package JMP version 12.1.0 (2015). This method applies a hierarchical cluster analysis, which chooses the pair of clusters (i.e., countries or regions) to merge at each step, based on the minimum value of the variance between subjects.

Table 3.1

Characters Used for the Cluster Production

Characters of the upper teeth	**Characters of the lower teeth**
I^2 Interruption Groove	I_1 Lingual tubercle
C^1 Distal Accessory	I_2 Lingual tubercle
C^1 Mesial Ridge	C_1 Distal Accessory
P^3-Accessory Cusp	P_3-Mesiolingual Groove
M^1 Cusp 4	P_4-Mesiolingual Groove
M^1 Cusp 5	P_4- "U" fissure pattern
M^1 Carabelli	P_4- "H" fissure pattern
M^2 Cusp 5	P_4- "Y" fissure pattern
M^3 Cusp 4	M_1 Cusp 6
	M_1 Cusp 7
	M_1 Deflecting wrinkle
	M_1 “X” fissure pattern
	M_1 “Y” fissure pattern
	M_1 “+” fissure pattern
	M_1 Mid Trigonid crest
	M_2 Cusp 6
	M_2 Cusp 7
	M_2 Deflecting wrinkle
	M_2“X” fissure pattern
	M_2 “Y” fissure pattern
	M_2 “+” fissure pattern
	M_2 Distal Trigonid crest
	M_2 Mid Trigonid crest
	M_3 Cusp 6
	M_3 Deflecting wrinkle
	M_3 “X” fissure pattern
	M_3 “Y” fissure pattern
	M_3“+” fissure pattern
	M_3 Mid Trigonid crest

Chapter 4: Results

In this chapter, I present results in the form of character frequencies, t-test results, and cluster analyses. Raw counts of characters are presented in Appendix A.

Character Frequencies

The results displayed in Table 4.1 provide counts of significant differences ($\alpha = 0.05$) resulting from country-by-country comparisons for each character. Results of country-by-country comparisons indicate that the most variable tooth is M^1 with the characters M^1 Cusp 5 (13 differences), M^1 Carabelli (12 differences) and M^1 Cusp 4 (6 differences) exhibiting the greatest number of significant differences when sites from different countries are compared. For M^2, Cusp 5 (8 differences) and Carabelli's cusp (2 differences) show regional variation, as does M^3 Cusp 4, (4 differences) and Cusp 5 (2 differences). For the upper canine, the mesial (8 differences) and distal accessory ridges (4 differences) show variation in relative frequency. P^3 shows greater regional variation in relative frequency than P^4, in the presence of a mesial and/or distal accessory cusp (8 differences), bifurcated essential crest (2 differences), and the presence of a mesial or distal accessory ridge (1 difference). P^4 varies between two countries each in the presence of a bifurcated essential crest, mesial/distal accessory ridge, and mesial/distal accessory cusp with 2 differences for each.

For the lower teeth, M_2 is the subject of the most variation in frequency in the presence of the “Y” fissure pattern (16 differences), “+” fissure pattern (14 differences), cusp 6 (14 differences), distal trigonid crest (8 differences), cusp 7 (7 differences) mid trigonid crest (6 differences). The next most variable tooth when performing comparisons between countries is M_3. This tooth shows significant differences in frequencies in the presence of the “+” fissure pattern (14 differences), cusp 6 (11 differences), mid trigonid crest (8 differences), “X” fissure pattern (8 differences), and “Y” fissure pattern (7 differences). The M_1 shows variation between countries in the frequency of the mid trigonid crest (16 differences), “Y” fissure pattern (13 differences), cusp 7 (10 differences), “X” fissure pattern (7 differences) and M_1 “+” fissure pattern (6 differences).

Among the premolar teeth, P_4 shows the most variation with between-country differences in the presence of the “Y” fissure pattern (14 differences), mesiolingual groove (13 differences), m “U” fissure pattern (12 differences), and “H” fissure pattern (7 differences). P_3 shows variation between countries in the relative frequency of the mesiolingual groove (8 differences), and I_2 varies in the frequency of the lingual tubercle (6 differences).

Table 4.1

Number of Significant Differences for Each Character (numerator) Calculated Over All Country-by-Country Comparisons (denominator).

Upper tooth Character	**Frequency**	**Lower tooth Character**	**Frequency**
M^1 Cusp 5	13/25	M_2 "Y"	16/46
M^1 Carabelli	12/28	M_1 Mid. trigonid crest	16/49
M^2 Cusp 5	8/28	M_3 "+"	14/31
C^1 Mesial	8/28	M_2 cusp 6	14/51
P^3 Accessory Cusp mesial/distal	8/19	M_2 "+"	14/46
M^1 Cusp 4	6/26	M_1 "Y"	13/49
C^1 Distal accessory ridge	4/24	P_4 Mesiolingual groove	13/32
M^3 Cusp 4	4/26	P_4 "Y" fissure pattern	12/36
I^2 Interruption groove	3/22	P_4 "U" fissure pattern	12/36
P^3 Bifur. Ess. Crest buccal/ Lingual	2/19	M_3 Cusp 6	11/33
P^4 Bifur. Ess. Crest buccal/lingual	2/21	M_1 Cusp 7	10/53
P^4 Accessory Ridge mesial/distal	2/16	P_3 Mesiolingual groove	8/25
P^4 Accessory Cusp mesial/ distal	2/19	M_2 Distal Trig. Crest	8/26
M^2 Carabelli	2/35	M_3 Mid. trigonid crest	8/34
M^3 Cusp 5	2/24	M_3 "X" fissure pattern	8/32
P^3 Accessory ridge mesial/distal	1/15	M_3 Defl. wrinkle	8/27
		P_4 "H" fissure pattern	7/36
		M_1 "X"	7/49
		M_2 Cusp 7	7/51
		M_3 "Y"	7/31
		I_2 Lingual tubercle	6/18
		M_1 "+"	6/39
		M_2 Mid. Trigonid crest	6/48
		C_1 Distal Accessory	5/31
		M_2 Defl. wrinkle	4/40
		M_2 "X"	3/47
		I_1 Lingual Tubercle	3/16
		I_1 Interrupt groove	1/16
		I_2 Interrupt groove	1/23

Country-by-Country Comparisons

Tables 4.2 through 4.8 provide the results of country-by-country comparisons of each of the 35 characters used in this analysis. In each table, blue cells with the number “1” indicate a significant difference in the relative frequency of the character between the two countries compared. Table 4.2 presents results of comparisons between Belgium and each of the eight other countries from which sites are evaluated in this study. Table 4.2 indicates that specimens from Belgium show the greatest number of significant differences in the frequency of dental characters from Croatia (26 characters) and France (19 characters). Belgium shows only a single difference, the frequency of the M_2 distal trigonid crest, with Germany and Poland.

Table 4.2

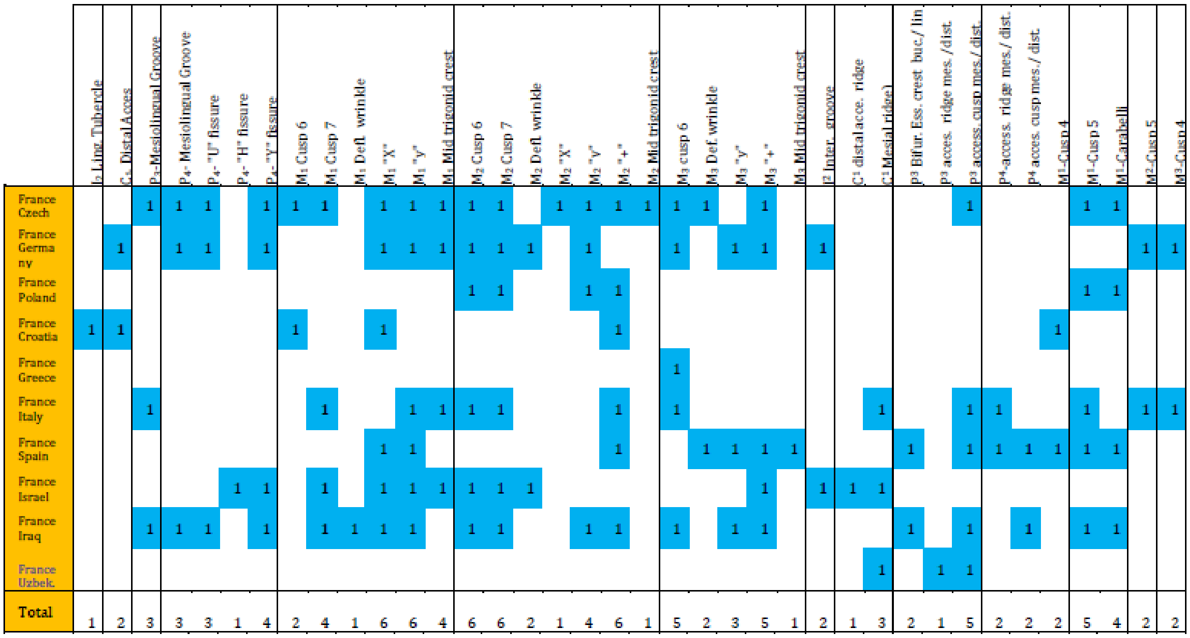
Significant Differences in Trait Frequencies between Belgium and Other Countries. Blue cells with the number “1” indicate significant frequency differences.

	I_1 Lingual . Tubercle	I_2 Lingual Tubercle	I_1 Interrupt. Groove.	I_2 Interrupt. Groove	C_1 Distal Accessory ridge	P_4- Mesiolingual Groove	P_4- "U" fissure	P_4- "H" fissure	P_4- "Y" fissure	M_1 Cusp 6	M_1 Cusp 7	M_1 Def. wrinkle	M_1 "X"	M_1 "Y"	M_1 "+"	M_1 Mid trig. crest	M_2 cusp 6	M_2 cusp 7	M_2 "Y"	M_2 "+"	M_2 Distal trig. crest	M_2 Mid trig. crest	M_3 Cusp 6	M_3 Defl. wrinkle	M_3 "X"	M_3 "+"	M_3 Mid trigonid crest	C^1 Distal accessory ridge	C^1 Mesial ridge	M^1 Cusp 4	M^1 Cusp 5	M^1 Carabelli	M^2 Cusp 5	M^2 Carabelli	M^3 Cusp 4
Belgium - Croatia	1	1		1	1	1	1				1	1		1	1	1	1		1	1	1	1	1	1	1	1		1	1		1		1	1	1
Belgium – France			1				1				1		1	1		1	1	1	1	1	1		1			1			1		1	1	1	1	1
Belgium - Israel								1	1				1								1		1				1								
Belgium - Czech								1								1					1														
Belgium - Iraq								1													1														
Belgium - Spain										1						1														1					
Belgium - Germany																					1														
Belgium - Poland																					1														
Belgium - Italy												1									1														
Total	1	1	1	1	1	1	2	3	1	1	2	2	2	2	1	4	2	1	2	2	8	1	3	1	1	2	1	1	2	1	2	1	2	2	2

Table 4.3 presents the results of character frequency comparisons between specimens from France and those from nine countries for which comparative samples were available. France differs has between 14 and 21 frequency changes differences with the other countries. It is to note that Spain and Belgium are similar with 3 differences. Table 4.5 and table 4.6 show a small difference (3) between Czech versus Italy and Germany versus Italy with 2 differences. Table 4.7 shows that Italy has little difference with Iraq (3 differences), Israel (2 differences) and Spain (3 differences). Table 4.8 indicates that Spain has 4 differences with Iraq and 7 differences with Israel while Iraq and Israel have 5 differences.

Table 4.3

Significant Differences in Trait Frequencies between France and Other Countries. Blue cells with the number "1" indicate significant frequency differences.



	I_2 Ling. Tubercle	C_1 Distal Acces	P_3- Mesiolingual Groove	P_4- Mesiolingual Groove	P_4- "U" fissure	P_4- "H" fissure	P_4- "Y" fissure	M_1 Cusp 6	M_1 Cusp 7	M_1 Defl. wrinkle	M_1 "X"	M_1 "y"	M_1 Mid trigonid crest	M_2 Cusp 6	M_2 Cusp 7	M_2 Defl. wrinkle	M_2 "X"	M_2 "y"	M_2 "+"	M_2 Mid trigonid crest	M_3 cusp 6	M_3 Def. wrinkle	M_3 "y"	M_3 "+"	M_3 Mid trigonid crest	I^2 Inter. groove	C^1 distal acce. ridge	C^1 Mesial ridge)	P^3 Bifur. Ess. crest buc./lin	P^3 acces. ridge mes./dist.	P^3 access. cusp mes./dist.	P^4-access. ridge mes./dist.	P^4 acces. cusp mes./dist.	M^1-Cusp 4	M^1-Cusp 5	M^1-Carabelli	M^2-Cusp 5	M^3-Cusp 4
France Czech			1	1	1		1	1	1		1	1	1	1	1		1	1	1	1	1	1		1							1				1	1		
France Germany		1		1	1		1				1	1	1	1	1	1		1			1		1	1		1											1	1
France Poland														1	1			1	1																1	1		
France Croatia	1	1						1			1								1															1				
France Greece																					1																	
France Italy			1						1			1	1	1	1				1		1							1			1	1			1		1	1
France Spain											1	1							1			1	1	1	1				1		1	1	1	1	1	1		
France Israel						1	1		1		1	1	1	1	1	1								1		1	1	1										
France Iraq			1	1	1		1		1	1	1	1		1	1			1	1		1		1	1					1		1		1		1	1		
France Uzbek.																												1		1	1							
Total	1	2	3	3	3	1	4	2	4	1	6	6	4	6	6	2	1	4	6	1	5	2	3	5	1	2	1	3	2	1	5	2	2	2	5	4	2	2

Table 4.4

Significant Differences in Trait Frequencies between Croatia and Other Countries. Blue cells with the number "1" indicate significant frequency differences.

	I_1 Lingual Tubercle	I_2 Lingual Tubercle	C_1 Distal Accessory	P_3-Mesiolingual Groove	P_4 Mesiolingual Groove	P_4- "U" fissure	P_4- "H" fissure	P_4- "Y" fissure	M_1 Cusp 7	M_1 "y"	M_1 "+"	M_1 Mid trigonid crest	M_2 Cusp 6	M_2 Defl. wrinkle	M_2 "y"	M_2 "+"	M_3 Cusp 6	M_3 Def. wrinkle	M_3 "X"	M_3 "y"	M_3 "+"	M_3 Mid trigonid crest	I^2 Inter. groove	C^1 distal acces. ridge	C^1 Mesial ridge)	P^3 Acces. cusp mes./ dist.	P^4 Bif. Ess. crest buc./	M^1-Cusp 4	M^1-Cusp 5	M^1-Carabelli	M^2-Cusp 5
Croatia - Greece																	1	1													
Croatia - Italy		1	1	1					1	1	1	1	1		1				1					1	1	1			1		
Croatia - Spain			1								1				1	1		1	1		1	1				1	1	1	1	1	1
Croatia - Iraq				1	1	1		1	1		1		1		1	1		1	1	1	1						1		1	1	1
Croatia - Israel	1	1		1			1	1	1	1	1	1		1				1			1		1	1	1						
Croatia- Uzbek.																									1			1			
Total	1	2	2	3	1	1	1	2	3	2	4	2	2	1	3	2	1	4	3	1	3	1	1	2	3	2	2	2	3	2	2

Table 4.5

Significant Differences in Trait Frequencies between Czech and Other Countries. Blue cells with the number "1" indicate significant frequency differences.

	I_1 Lingual Tubercle	I_2 Lingual Tubercle	P_3-Mesiolingual Groove	P_4- Mesiolingual Groove	P_4- "U" fissure	P_4- "H" fissure	P_4- "Y" fissure	M_1 Cusp 7	M_1 "y"	M_1 "+"	M_1 Mid trigonid crest	M_2 Cusp 6	M_2 "X"	M_2 "y"	M_2 "+"	M_2 Mid trigonid crest	M_3 "X"	M_3 "+"	M_3 Mid trigonid crest	M^1-Cusp 5	M^1-Carabelli
Czech - Croatia	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1		1	1
Czech - Italy	.								1							1		1			
Czech - Spain	.			1	1		1				1					1					
Czech- Israel	.			1	1	1							1						1		
Total	1	1	1	3	3	1	2	1	2	1	2	1	2	1	1	3	1	2	1	1	1

Table 4.6

Significant Differences in Trait Frequencies between Germany and Other Countries. Blue cells with the number "1" indicate significant frequency differences.

	I_1 Lingual tubercle	I_2 Lingual tubercle	P_4- Mesiolingual Groove	P_4- "U" fissure	P_4- "H" fissure	P_4- "Y" fissure	M_1 "y"	M_1 "+"	M_1 Mid trigonid crest	M_2 Cusp 6	M_2 Def. wrinkle	M_2 "y"	M_2 "+"	M_3 Cusp 6	M_3 Def. wrinkle	M_3 "X"	M_3 "y"	M_3 "+"	M_3 Mid trigonid crest	I^2 Inter. Groove	M^2-Cusp 5
Germany- Croatia	1	1	1	1		1	1	1	1	1	1	1	1		1	1	1	1		1	1
Germany- Italy																	1	1			
Germany - Spain			1						1												
Germany - Israel			1		1								1	1					1		
Total	1	1	3	1	1	1	1	1	2	1	1	1	2	1	1	1	2	2	1	1	1

Table 4.7

Significant Differences in Trait Frequencies between Italy and Other Countries. Blue cells with the number "1" indicate significant frequency differences.

	M_1 Def. wrinkle	M_1 Mid trigonid crest	M_2 "y"	M_3 "Y"	M_3 "+"	M^1-Cusp 5	M^1-Carabelli
Italy - Iraq	1			1	1		
Italy - Israel			1		1		
Italy - Spain		1			1	1	
Italy - Poland							1
Total	1	1	1	1	3	1	1

Table 4.8

Significant Differences in Trait Frequencies between Poland, Greece, Spain, and Iraq and Other Countries. Blue cells with the number "1" indicate significant frequency differences.

	P_3-Mesiolingual Groove	P_4-Mesiolingual Groove	P_4 "U" fissure	P_4 "H" fissure	P_4 "Y" fissure	M_1 Mid trigonid crest	M_2 Cusp 6	M_2 "y"	M_2 "+"	M_3 Cusp 6	M_3 Mid trigonid crest	C^1 Distal acce. ridge	M^1-Cusp 4	M^1-Cusp 5	M^1-Carabelli	M^2-Cusp 5
Poland - Croatia							1	1	1					1	1	1
Poland - Spain							1									
Poland - Iraq								1								
Total							2	2	1					1	1	1
Greece - Iraq										1	1					
Total										1	1					
Spain - Iraq		1	1		1								1			
Spain - Israel	1			1	1	1		1			1	1				
Total	1	1	1	1	2	1		1			1	1	1			
Iraq - Israel		1	1	1				1			1					
Total		1	1	1				1			1					

Results of Ward cluster analysis of the six countries for which sample sizes permitted comparison are presented in Figure 4.1. Results demonstrate that France and Croatia are quite similar, with differences in the relative frequencies of only six characters (see Table 4.3) and a minimum variance of 1.9. On the contrary, the number of significant differences in the relative frequencies of dental characters (n = 19) between France and Belgium are reflected in the results of the Ward cluster analysis, where these countries demonstrate minimum variance of 5.3. The cluster "France-Croatia" joins with another cluster that consists of Spain and Israel. These later countries join at a minimum variance of 4.2 and their cluster joins with France with a variance minimum of 4.6. Aside from Belgium, which shows the greatest difference in the relative frequency of characters, Iraq is the most distant joiner with a minimum variance of 5.2.

The countries such as Germany, Poland, Czech, Greece and Uzbekistan could not be considered because they did not have a value for a certain amount of characters and the Ward system could not calculate the variance.

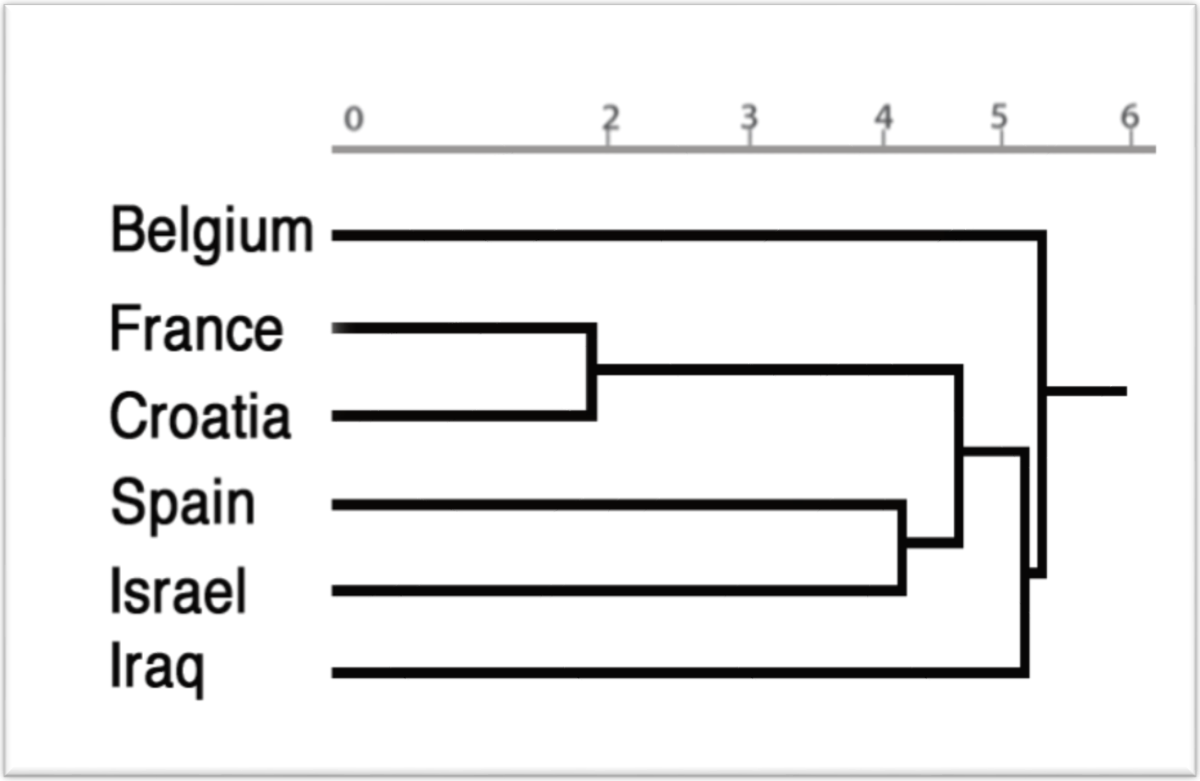


Figure 4.1. Dendrogram with hierarchical clustering of countries Belgium, France, Croatia, Spain, Israel, and Iraq.

Comparisons of Broader Regions

North, South, East. Results of character frequency differences between the North (France, Belgium, Germany, Czech, Poland), South (Spain, Croatia, Italy, Greece), and East (Israel, Iraq, Uzbekistan) regions are presented in Table 4.9. These results indicate that the greatest numbers of significant differences in character frequencies occur between the East region and the other two regions, where the East and North differ in the frequencies of sixteen characters, and the East and South differ in the frequencies of eighteen characters. In contrast, the North and South regions differ in the relative frequencies of only four characters.

When distances between North, South, and East regions are evaluated using the Ward's clustering method, the resulting dendrogram reflects the differences in trait frequencies elucidated through the t-tests. The North and South cluster at a distance of 4.8. The East region is further separated from the North at a distance of 7.3.

Table 4.9

Significant Differences in Trait Frequencies between North, South, East Region

	I_1 Ling. T	I_2 Ling. T	C_1 dist. Acc.	P_3-ML Groove	P_4- "H" fissure	P_4- "Y" fissure	M_1 cusp 7	M_1 X	M_1 y	M_1 +	M_2 cusp 6	M_2 cusp 7	M_2 Defl. wrinkle	M2 +	M_2 Mid trig. crest	M_3 cusp 6	M3 Defl. wrinkle	M_3 y	M_3 +	I^2 Inter. groove	C^1 Mesial ridge	M^1-C5	M^1-Ca	M^2-C5	M^3-C4
N-S		1	1					1								1									
N-E					1	1	1	1	1		1	1	1		1			1		1	1	1	1	1	1
S-E	1	1		1		1	1		1	1	1		1	1	1		1	1	1		1	1	1	1	

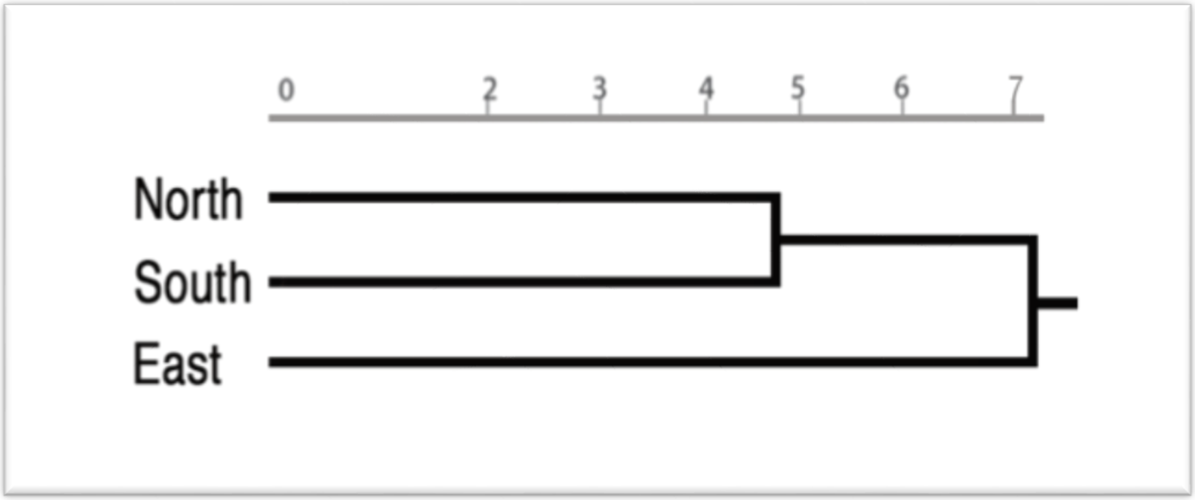


Figure 4.2. Dendrogram showing hierarchical clustering of North (France and Belgium, Germany, Czech, Poland), South (Croatia, Italy, Greece, Spain), and East (Israel, Iraq, Uzbekistan) regions.

Regions European, Mediterranean and Spain. I cannot exclude the possibility that these results may be influenced by sample size, so to control this result I joined Belgium to France to form a region called Europe West, and left Spain by itself. I made a region called Mediterranean center (Croatia, Italy and Greece), and a region called Europe Center, composed of Germany, Poland and Czech. Finally, I created a region called Mediterranean East that consisted of Israel, Iraq and Uzbekistan.

The clustering history gives 4 clusters, composed of Europe west and Mediterranean Center in the same cluster (distance: 3.6), Europe Center with Europe West-Mediterranean Center (distance > 4.9), Mediterranean East is the next to join (distance > 5.7) and finally Spain, which joins at a distance greater than 6.2.

Table 4.10

Significant Differences in Trait Frequencies between Geographic Regions. Green cells with an "x" indicate significant frequency differences

	I^1 Ling. T	I^2 Ling. T	C^1 .dist. Acc	P^3 -ML Groove	P^4 -ML Groove	P^4 -"H" fissure	P^4 -"Y" fissure	M^1 cusp 7	M^1 Deflecting wrink	M^1 X	M^1 y	M^1 +	M^1 Mid trigonid cre	M^2 cusp 6	M^2 cusp 7	M^2 Deflecting wrink	M^2 X	M^2 y	M^2 +	M^2 Mid trigonid cre	M^3 cusp 6	M^3 Deflecting wrink	M^3 X	M^3 y	M^3 +	M^3 Mid trigonid cre
E. West E. Center			x	x	x								x		x										x	
E. West Spain				x						x	x							x	x		x				x	x
E. West Med. Center		x	x						x										x							
E. West Med. East							x		x	x	x			x	x	x				x				x	x	
W. Center Spain					x	x							x					x								
E. Center Med. Center	x	x	x	x	x							x	x									x			x	
E. Center Med. East			x		x	x										x										
Spain Med. Center			x	x							x	x						x	x			x	x	x	x	x
Spain Med. East			x	x		x	x																x	x		x
Med. Center Med- East	x	x		x			x	x			x	x		x		x			x	x		x		x	x	

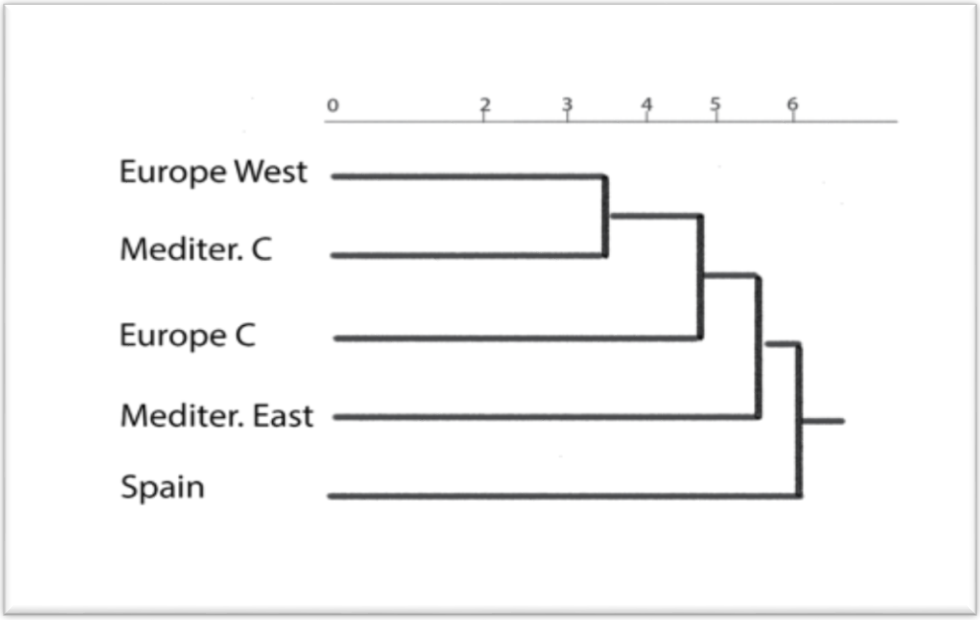


Figure 4.3. Dendrogram with hierarchical clustering of Western Europe (France and Belgium), central Europe (Germany, Czech, Poland), Mediterranean region center (Croatia, Italy, Greece), Mediterranean region east (Israel, Iraq, Uzbekistan) and Spain.

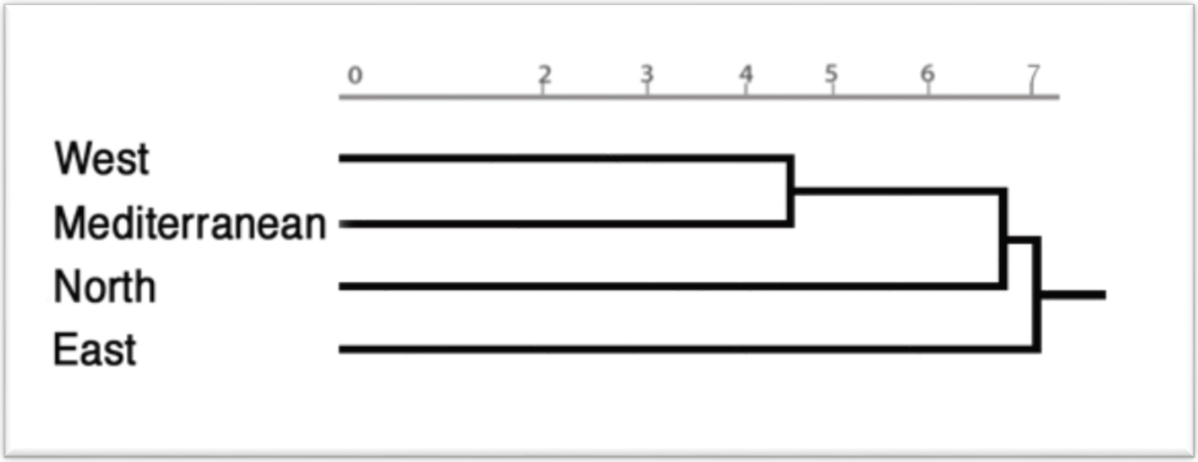


Figure 4.4. Dendrogram with hierarchical clustering of Western Europe (France and Belgium), northern Europe (Germany, Czech, Poland), Mediterranean (Croatia, Italy, Greece, Spain), eastern region east (Israel, Iraq, Uzbekistan).

Because most Spanish sites are geographically on the east coast, Figure 4.4 includes Spain within the Mediterranean group (Croatia, Italy, Greece) to evaluate whether there is an impact with the clustering. In this case, I added Spain to the "Mediterranean Central" group to form a new grouped called Mediterranean. Israel, Iraq, and Uzbekistan form a group called "East." The clustering history presented in Figure 4.4 shows 3 clusters, composed of western Europe (West) and Mediterranean in the same cluster (distance: 4.5), northern Europe (North) joins this initial cluster (distance: 6.7) followed by the "East" (distance: 7).

Chronological Approach

OIS 5. Results of chronological analyses are presented in Tables 4.11 through 4.13. Table 4.11 shows that, during OIS 5, the East region differs from the West and Mediterranean regions. East differs from West in the relative frequencies of 18 characters and it differs from the Mediterranean in the relative frequencies of 13 characters. The West and Mediterranean regions are similar, differing in the relative frequencies of only five characters.

Table 4.11

Characters Difference in OIS 5 between Regions

	West-East	Center-East	West-Center
C_1 Distal accessory ridge	1		
P_3-Transverse crest		1	
P_3 Lingual accessory cusp	1	1	
P_4 Mesiolingual Groove	1	1	1
P_4 "U" fissure pattern	1	1	1
P_4 "Y" fissure pattern	1	1	1
M_1 Cusp 7		1	
M_1 Deflecting wrinkle		1	
M_1 “Y” fissure pattern		1	
M_1 “+” fissure pattern	1	1	1
M_1 Mid trigonid crest	1	1	
M_2 Cusp 6	1	1	
M_2 “Y” fissure pattern			
M_2 “+” fissure pattern			
M_2 Distal trigonid crest	1		
M_2 Mid trigonid crest	1		1
M_3 Deflecting wrinkle	1		
M_3 “X” fissure pattern		1	
M_3 “+” fissure pattern		1	
I^1 Interruption groove	1		
C^1 Distal accessory ridge	1		
$C^{1.}$ Mesial ridge	1		
P^3 Bifurcation. Essential crest buccal/ lingual	1		
P^3 Accessory ridge mesial /distal	1		
P^3 Accessory cusp mesial/ distal	1		
M^1 Carabelli	1		
Total	18	13	5

Figure 4.5. Map OIS 5. The sites of Neanderthal are spread out far north (Ehringsdorf) in Germany and Stajnia in Poland.

OIS 4. Table 4.12 indicates that the western region stays different from the eastern region with 10 differences and that it is mainly the P_4 and the molars that are touched by changes. What is new is that the Mediterranean center seems to separate from the west region with 7 differences, which concern the molars, mainly M_1 (cusp 6, cusp 7, Deflecting wrinkle, “Y” fissure pattern and Mid trigonid crest). It shows the similarity between region Europe center and east region with only 2 differences concerning the feature Cusp 6 for M_1 and M_3.

Table 4.12

Characters Frequencies Change in OIS 4 between Regions

	West-East	Center-East	West-Center
C_1 Distal accessory ridge	1		
P_4 Mesiolingual Groove	1		
P_4 "H" fissure pattern	1		
P_4 "Y" fissure pattern	1		
M_1 Cusp 6		1	1
M_1 Cusp 7	1		1
M_1 Deflecting wrinkle			1
M_1 “Y” fissure pattern	1		1
M_1 Mid trigonid crest			1
M_2 Deflecting wrinkle	1		
M_3 Cusp 6		1	1
M_3 “Y” fissure pattern	1		
M_3 “+” fissure pattern	1		
M_3 Mid trigonid crest			1
M^3 Cusp 4	1		
Total	10	2	7

Figure 4.6. Map OIS 4. During this cold period, we have no Neanderthal sites in the north. The southwest of France is still occupied as far north as the Grotte de Boccard.

Table 4.13

OIS 3 West and Center Europe, Spain, Mediterranean and East Region

	West-Spain	Center-Spain	West-Center	West-Mediter.	Center-East
P_3-Mesiolingual groove	1				
P_3 Distal accessory cusp		1			
P_4 Mesiolingual Groove			1		
P_4 "U" fissure pattern		1	1		
P_4 "Y" fissure pattern		1			
M_1 Cusp 6			1		
M_1 “X” fissure pattern	1		1	1	
M_1 “Y” fissure pattern			1	1	
M_1 Mid trigonid crest		1	1		
M_2 Cusp 6			1	1	
M_2 Cusp 7			1	1	
M_2 “X” fissure pattern			1		
M_2 “Y” fissure pattern			1		
M_2 Mid trigonid crest			1	1	
M_3 “X” fissure pattern			1		1
M_3 “+” fissure pattern			1		
$C^{1.}$ Mesial ridge				1	
P^3 Bifurcation Essential crest buccal/ lingual	1				
P^4 Bifurcation Essential crest buccal/ lingual	1				
P^4 Accessory ridge mesial/ distal	1				
M^1 Cusp 5	1				
M^1 Carabelli	1				
M^2 Cusp 5				1	
M^2 Carabelli			1	1	
Total	7	4	14	8	1

OIS 3. In table 4.13, the western region, the teeth P_4, M_1, M_2, M_3 have 7 differences with Spain, 14 with European center (Germany, Czech, Poland). M_1, M_2 and M^2 are teeth that are subject of frequencies changes with 8 between Mediterranean (Croatia, Italy, Greece) and

the western region. It is noteworthy that the Mediterranean region has only 1 difference with the eastern region.

Figure 4.7. Map OIS 3. After the cold period of OIS 4, Sites such as Feldhofer in Germany are back in the north as well as Ochoz and Sipka in Czech Republic.

Analyzes of France's sites located in the 3 OIS. Considering that France contains sites that date to each of the three OIS periods, it is possible to evaluate evolutionary change through time within a relatively confined geographic region. Table 4.13 presents comparison of character frequencies between French sites of different time periods, as indicated by oxygen isotopes. Between OIS 5 and OIS 4 there are frequency changes in eight characters. The premolar P_4 with the "U" and "Y" fissure pattern, the molar M_1 Mid trigonid crest and the molar M_2 with the "Y" and "+" fissure pattern. On the upper teeth, it is the incisor I^2 with the Interruption groove and the molar M^3 with the cusp 4. At the end of OIS 4, the following 7 characters are modified: the canine C_1 with the distal accessory ridge, the premolar P_4 mesiolingual groove, M_1 cusp 7, M_2 "+" fissure pattern, M_3 Mid. Trigonid crest, and on the upper teeth, I^2 Interruption groove, and P^3 accessory cusp mesial/distal. Between France OIS 3 and OIS 5 there is 10 features changed: 1) P_4 Mesiolingual groove; and, the "U" and "Y" fissure pattern; 2) the molar M_1 Mid. trigonid crest, and M2 cusp 6 and M_2 "Y". On the upper teeth, it is the canine C^1 distal accessory ridge, P^3 bifurcation Essential Crest Buccal/ lingual, the P^3 accessory ridge and the molar M^1 with Carabelli (Table 4.13).

Table 4.14

France OIS 5, 4, 3 Modifications

	C_1 distal accessory ridge	P_4 ML Groove	P_4 "U" fissure	P_4 "Y" fissure	M_1 cusp 7	M_1 Mid trigonid crest	M_2 cusp 6	M_2 y	M_2 +	M_3 Mid trigonid crest	I^2 Interruption groove	C^1 distal accessory ridge	P^3 Bifur. Ess. crest buc./ ling.	P^3 acces. ridge mes. /dist.	P^3 access. cusp mes./ dist.	M^1 -Cara	M^3 cusp 4	
France3- France4	1	1			1				1	1	1				1			7
France3- France5		1	1	1		1	1	1				1	1	1		1		10
France4-France5			1	1		1		1	1	1	1						1	8
Total	1	2	2	2	1	2	1	2	2	2	2	1	1	1	1	1	1	25

Figure 4.8. France OIS 5. The few sites of France that had teeth available for our study.

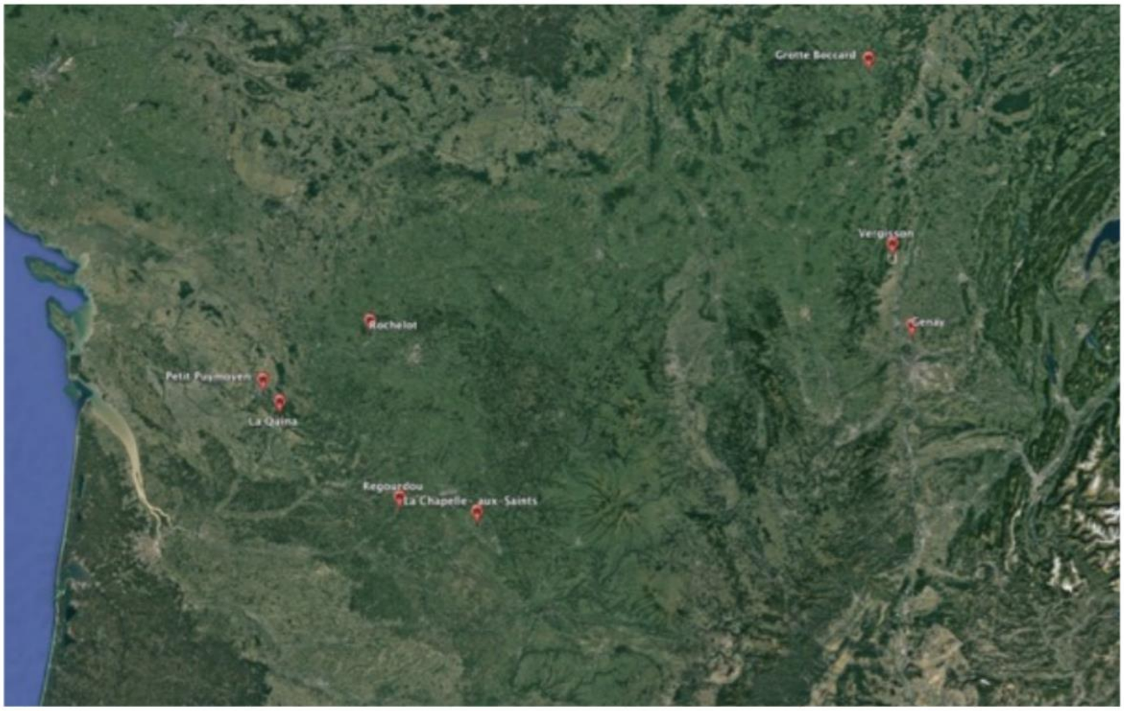


Figure 4.9. France OIS 4. Note that Grotte Boccard was one of the most northern sites.

Figure 4.10. France OIS 3. St. Cesaire, Moustier and Arcy sur Cure are among the sites that are most known.

Chapter 5: Discussion and Conclusion

Discussion

Characters (Table 4.1). During the period from OIS-5 to OIS-3, most character frequency changes occur on the molars and premolars. Among the upper teeth, M^1 shows the most variation through time, with changes in the frequencies of cusp 5 (13), Carabelli's cusp (12), and cusp 4 (6). The M^2 also shows relatively high numbers of frequency shifts in cusp 5(8) and Carabelli's cusp (2), while M^3 shows changes in the frequencies of cusps 5 (2) and cusp 4 (4). These high amount of variability, particularly concerning cusp 5 and the Carabelli's trait for M^1 and M^2, do not support the commonality that Bailey (2006) shows even if there might exist a trend that is consistent with Bailey's high frequency indication concerning M^1 cusp 5 (64%) and Carabelli'trait (68 %) and M^2 cusp 5 (68%) and Carabelli's trait (50%). Hillson (2003) contends that Carabelli's cusp is common among M^1, less common with M^2 and rare in M^3, my results give me the same proportion for the Neanderthals.

For the lower teeth, M_1 and M_2 are the teeth with the most variation through time. The fissure pattern with the most subject of changes is the "Y" fissure pattern 16 time for M_2, 13 for M_1 and 7 with M_3; "+" 14 for M_3, 14 for M_2 and 6 for M_1 while "X" fissure pattern occurs 8 for M_3, 7 time for M_1 and 3 for M_2. M_2 Cusp 6 has 14 differences and M_3 has 11 differences. It is also to note that M_1 Mid trigonid crest has 16 differences. These high amount of variability, especially concerning "Y" fissure pattern for M_1 and M_2, Mid trigonid crest for M_1 and cusp 6 for M_2 do not support the commonality that Bailey (2006) indicates even if there might be a trend that is consistent with Bailey's high frequency concerning M_1 "Y" fissure pattern (98%), M_1 Mid trigonid crest (98%) and M_2 “Y” fissure pattern (75%) and M cusp 6 (50%). In contrast Hanihara (1967) identified a “caucasoid dental complex” and indicated that cusp 6 was a low frequency feature. In this study, cusp 6 on M_1 and M^1 are low frequency features; this conforms with Hillson’s (2003) characterization of modern *Homo sapiens*. Beside the molars, P_4 has a high difference with the fissure patterns: 14 with “Y” fissure pattern, 12 with “U” fissure pattern and 7 with the “H” fissure pattern. The feature mesiolingual groove is subject to changes in frequency with 13 changes for P_4 and 8 for P_3. Changes in the frequencies of molar characters could be interpreted as an adaptive response to dietary change due to the environmental change (Clement et al., 2012), the same may be true for changes in the frequencies of premolar characters.

Countries. Before analyzing the result of the comparison of the countries, I must underline the following facts. First, France has 145 teeth and Croatia 183 teeth, which make for both 67 % of all the teeth, this discrepancy might have an impact over the result. Second, Croatia is represented by only 1 site Krapina, situated near Italy, while France has about 20 sites throughout. Third, beside their geographical isolation due to the Pyrenees’ barrier, the specimens from Spain are practically all from the south-east coast of Spain: Zaffaraya (Barroso and Hublin, 1994; Barroso and de Lumey, 2006), Las Palomas (Walker et al. 2012), Cova Negra (Arsuaga et al. 1989; Walker et al. 1998), Cova Forada, Los Moros de Gabas and Gibraltar and are classified in the OIS 3. With JMP, I used the Ward method and as mentioned in Chapter 3 if the number of objects are unequal, the Ward method does not work well. It is the case with the countries at the exception of France and Croatia. If we analyze Figure 4.1, France–Croatia are in the same cluster and this similarity is confirmed by

Table 4.3 where these countries have only 6 characters' frequency (I_1, I_2 lingual tubercle, M_1 cusp 6 and "X", M_2 "Y" and M^1cusp 4). France and Croatia, expressing low variance, are in the same cluster, it is the same for Israel and Spain. Considering the low number of specimens for Belgium and Spain, it seems logical to increase regional sample sizes by joining Belgium to France in a western region, Iraq with Israel in eastern region and Spain in a southern region with Croatia, Italy and Greece.

Regions. Table 4.9 and figure 4.12, comparing the northern, the southern and the eastern regions demonstrate that the regions North are South similar to each other and different from the East. Tables 4.2 through 4.8 demonstrate that the east region, consisting of Israel, Iraq and Uzbekistan is consistently different from the other regions. One possible explanation for this distinction may be that there was a west to east morphological cline among Neanderthals created by a combination of isolation by distance and admixture with modern humans (Hambücken 1997; Voisin 2006, 2011, 2012). The hypothesis states that before the spread of *Homo sapiens* into Europe, the Neanderthals, throughout Europe and the Near East, were connected by gene flow (Voisin 2006). When Neanderthals arrived in western Europe, gene flow between western and eastern Europe became limited. When modern humans began moving west, they first encountered Neanderthals with whom they could interbreed. As they moved west, increased genetic distance between *H. sapiens* and classic Neanderthal populations precluded interbreeding (Hambücken 1997; Voisin 2006, 2011, 2012). If we consider Figure 4.1, Spain is in the same cluster as Israel with the distance 4.2, while Belgium and Iraq cluster with France at distances of 5.3 and 5.2 respectively. After group in Belgium with France, I realized that Spain was still in a standalone situation

(Figure 4.3), so I joined Spain to the southern group with Croatia, Italy and Greece to produce the dendrogram (Figure 4.4) based on 4 regions: West, Mediterranean, North and East. West and Mediterranean are in the same cluster, so we could consider we have 3 regions, as we see with the comparison of the north, south and east region (Figure 4.9). This supports the hypothesis of Hambücken (1997) and Fabre et al. (2009) concerning the existence of at least 3 distinct, regional, Neanderthal populations.

Chronological Approach: OIS 5, 4, 3

OIS 5 (from 130,000 years to 90,000 years ago). During OIS 5, there is a territorial extension of the Neanderthals over the Near East and central Asia (Condemi, 2016). Table 4.11 shows that the western region, with 18 differences, and the center region, with 13 differences, are both different from the East region, while they have only 5 differences between them. This suggests that there was a certain homogeneity between the west and the center and that during the warm climate in southern and central Europe of OIS 5, the Neanderthals were in position to extend their hunting and gathering territories farther north and east during this period (Bar Yosef and Vandermeersch 1991; Condemi 2007). Condemi (2016) suggests that this territorial extension may have seen, for the first time, the expansion of Neanderthals from southern and central Europe to beyond Eastern Europe and into the middle East and southern Siberia. During this time (OIS 5), the Neanderthal population size is estimated to have peaked at perhaps as high as 70,000 individuals. This is likely made possible by an abundance of food (Bocquet-Appel and Degioanni 2013; Pruefer et al. 2014; Condemi 2016). Evidence for this increase in population size is seen in the increased number of sites and the subsequently large dental sample (245 teeth).

OIS 4 (90,000 years to 57,000 years ago). OIS 4 begins around 90,000 years ago and reaches its glacial maximum around 66,000 years ago. This glacial maximum lasted for 5000 years (Van Andel and Davies 2003). During this time, the glaciers reached the northern Baltic and the north of Belgium. Northern European environments were dominated by tundra and cold steppe. One can imagine that the Neanderthals, following the herds, slowly moved south into unglaciated regions, such as southwest France, as during this time, Neanderthal sites in the north disappeared and the eastern sites are reduced in number. A reduction in the available sample sizes of dental specimens for this research from 245 specimens dating to OIS 5 to 93 specimens dating to OIS 4 may reflect this change in distribution and reduction in Neanderthal population size.

Table 4.12, indicates that there is a separation between the western region, containing sites situated mainly in the southwest of France, from the Mediterranean Center, containing Italy and Greece. Table 4.13 demonstrate that the dentitions of Neanderthals in France remain constant during OIS 5, 4, and 3. Thus, France may have served as a refuge during the cold periods as it maintained environmental consistency from OIS 7 through OIS 4 (Condemi, 2010). This supports Vandermeersch's (1987) view concerning France's continuous population with local variability.

Table 4.15 indicates a general decrease in frequency changes from OIS 5 to OIS 4. This may reflect a general decrease of the Neanderthal population. In detail, if we compare frequency changes between the West and East regions, we see that there are eight fewer changes in OIS 4 than in OIS 5. This may be related to the disappearance of northern European sites during the OIS 4 (France, Belgium, Germany, Poland, Czech). The comparison of West and Center (Spain, Croatia, Italy, Greece) regions indicate that the limited change in frequency (2 character frequencies change) could indicate that there is a certain stability in the south of Europe. This could be the consequence of the stability of southwest of France. When comparing Europe Center with East, the spectacular decrease from 13 to 2 frequency differences could be explained by population movement along the coast with perhaps some interbreeding, with migrants coming from the east (Hambücken 1997; Voisin 2006; Vandermeersch and Garralda 2011; Churchill 2014).

Table 4.15

Summary of the Regional Frequency Change between OIS 5 and OIS 4

	OIS 5	OIS 4
West - East	18	10
West - Center	7	5
Center- East	13	2

OIS 3 (57,000 years to 29,000 years ago). OIS 3 begins approximately 57,000 years ago and persists until 29,000 years ago. It is during this period that *Homo sapiens* arrives in Europe and the Neanderthals go extinct (Condemi 2016). Despite a brief decline around 53,000 years ago, possibly indicative of a cold steppe situation, the temperatures tend to rise during OIS3 (Allen et al. 2000). Under the influence of these mild temperatures, Neanderthals expand their range prior to their disappearance around 37,000 years ago. After the cold period of OIS 4, the warmth of the OIS 3 period provoked a Neanderthal population expansion, but, contrary to what happened during OIS 5, this expansion was limited to Europe center, Mediterranean and East regions (Hambücken 1997; Van Andel et al. 2003; Voisin 2006; Vandermeersch and Garralda 2011).

Table 4.13 shows 14 character frequency differences between Europe West and Europe Center during OIS 3. This suggests the presence of different Neanderthal populations in Europe center (Germany, Poland and Czech) and Europe West. This is consistent with the suggestion of Van Andel et al. (2003), who contends that the “re-colonization” of Neanderthals into north-central and Eastern Europe could have been initiated from the East, using the valleys of the big rivers such as the Danube, the Rhine or the Main, and the river systems of Ukraine. It is interesting that Europe center and Mediterranean center make a homogeneous group (From Germany to Italy) with only 1 character difference (see Figure 4.13).

Results presented in table 4.13 indicate that Europe west and Spain form a homogeneous group. It is reasonable to suggest that Spain and western Europe, due to their isolation, maintain their own Neanderthal group, isolated from H*omo sapiens* populations that were already present in Europe during this time period (Trinkaus et al. 2006; Benazzi et al. 2011; Condemi 2016). This isolation could be due to the density of the forest and high elevation of the Massif Central in the southwest of France. The south of France is bordered by the Pyrenees mountains that stretch from the shores of the Mediterranean Sea on the east to the Atlantic Ocean on the west and in the center, reaches about 80 miles in width. Continuity among the western European Neanderthals, including those from Spain, along with their differences from Neanderthals from other regions might result from the lack of admixture between Neanderthals from Western Europe and *H. sapiens.*

Conclusion

This research has demonstrated that the molars are the teeth that exhibit the most frequency changes. More precisely it is "+" and the "Y" fissure pattern of M_1, M_2 , M_3 ; Cusp 6 for M2, M3 and Mid trigonid crest for M_1 are subject of changes as well as cusp 5 and Carabelli's cusp for. M^1 and M^2. My results have established that the high amounts of variability, concerning all these traits do not support the commonality of Bailey (2006) even if there might exist a trend that is consistent with high frequency that Bailey indicates. Hillson (2003) contends that Carabelli's cusp is common among M^1, less common with M^2 and rare in M^3, my results give me the same distribution for the Neanderthals.

The P_4 also has high frequency changes with cusps 6 and 7 as well as the mesiolingual groove and the "Y" fissure pattern. I should underline that the molar, being more numerous (more than 50% of the teeth) might have an impact on the results.

Evaluation of dental frequencies between countries and larger regions allowed me to distinguish four Neanderthal subgroups, a western subgroup consisting of individuals from France and Belgium, a central subgroup with Neanderthals from Germany, Czech and Poland, a Mediterranean subgroup consisting of individuals from Spain, Croatia, Italy and Greece and an East subgroup consisting of individuals from Iraq, Israel and Uzbekistan (Bailey et al. 2008). This analysis confirms the Fabre et al. (2009) subdivision of the Neanderthal population, and adds resolution. Whereas Fabre et al. (2009) hypothesized the existence of a cohesive, North population, dental data support the subdivision of this region into western and central regions. This supports the east-west cline gradient hypothesis of different authors

(Vandermeersch 1981; Condemi 1988; Trinkaus 1998; Condemi 1992; Voisin 2006; Churchill 2014).

The chronological approach, gave me some information concerning the Neanderthal movements during the OIS 5 to OIS 3 periods. Based on the number of specimens I had, I could make some hypotheses regarding the increase or decrease of the Neanderthal population size. Sample sizes of dental specimens from each OIS, coincide with hypothesized population sizes, where 50% of the specimens analyzed date to OIS 5, a large population, 20% date to OIS 4, corresponding to a decreased Neanderthal population, and 30% date to OIS 3, thus suggesting an increase in population size during OIS 3. The OIS 4 and OIS 3 analyses indicate that the southwest of France had a stable and homogeneous Neanderthal population from OIS 5 through OIS 3, and that during OIS 4, some Neanderthals may have moved along the coast, where perhaps they may have contacted and, eventually interbreed with, migrants coming from the east. The main result shows also that during OIS-3, the Western Europe Neanderthals are different form the East Neanderthals because these have already been in contact with *Homo sapiens* (Condemi 2016). These last two points suggest that there may be a relationship between movement of the Neanderthals and climate changes, a retraction to the southwest of France and the Mediterranean coast during OIS-4 and a rapid but limited expansion during OIS-3. Based on my results concerning the differences between Europe West and Europe Center, this expansion could have been initiated from the east, which is consistent with the “re-colonization” suggested by Van Andel et al. (2003) and Voisin (2006).

Despite the small number of specimens and their disparity, which is often the case in paleolithic, the results that I have obtained, show that the biodistance method is robust and valid. It supports previous research that used other methods (Vandermeersch 1981; Condemi 1988; Trinkaus 1998; Condemi 1992; van Andel et al. 2003; Voisin 2006; Churchill 2014; Condemi 2016), and adds resolution to our understanding of Neanderthal evolution across space and through time. In this perspective, future studies should join the sites regionally, based on their coordination and enlarge the research period to OIS 7. This last point is based on recent discoveries such as the cave of Bruniquel in France, that indicated the Neanderthal were more advance than what we thought.

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Appendix

Incisors Counting

Neanderthal sites	I1 convexity	I2	I1 shoveling	I2	I1 Ling. Tubercle	I2	I1 Inter. groove	I2
Belgium								
Spy 1922-1 sp. 2	1	1	1	1	1	1	0	0
Croatia								
Krapina D nr 54		1		1		0		0
Krapina E nr 55	1	1	1	1	0	0	0	0
Krapina E nr 49	1		1		1		0	
Krapina F nr 50	1	1	1	1	1	1	0	0
Krapina H nr 58	1	1	1	1	1	1	0	0
Krapina J Nr 59	1	1	1	1			0	0
Krapina 199	1		1		0		0	
Krapina 198		1		1		0		0
Krapina 196		1		1		1		
Krapina 195	1		1		1		0	
Krapina 160		1		1		1		1
Krapina 159		1		1		1		0
Krapina 157	1		1		1		1	
Krapina 155	1		1		1		1	
Krapina 148		1		1		1		1
Krapina 133	1		1		1		0	
Krapina 132	1		1		1		1	
Krapina 131		1		1		1		0
Krapina 130		1		1		1		1
Krapina 129	1		1		1		0	
Krapina 128		1		1		1		0
Krapina 127		1		1		1		0
Krapina 126	1		1		1		1	
Krapina 125		1		1		1		1
Krapina 124		1		1		1		
Krapina 123	1		1		1		1	
Krapina 122		1		1		1		1
Krapina 95		1		1				
Krapina 94	1		1		1			
Krapina 93	1		1					
Krapina 92	1		1		1			
Krapina 90		1		1				1
Krapina 74	1		1		1		0	
Krapina 73	1		1					
Krapina 71		1		1		0		0
Krapina 70	1		1		0		0	
Krapina 57		1		1				
Vindija 201 Vi 201		1		1	1			0
Vindija 286 Vi 286		1		1				
Vindija 289 Vi 289		1		1		1		1
Vindija 290 Vi 290	1		1		1		0	

Neanderthal sites	I1 convexity	I2	I1 shoveling	I2	I1 Ling. Tubercle	I2	I1 Inter. groove	I2
Czech								
Ochoz	1						0	0
Sipka	1	1	1	0	1	1	0	0
France								
Arcy-I2 3-A nr 19		1		1		1		0
Arcy-I2 3-B nr 23		1		1				0
Arcy-I2 5 nr 11		1		1		1		0
Arcy-I2 9-U		1		1		1		1
Arcy sur 1977-2-9	1	1	1	1				
Arcy sur 1977-2-8	1	1	1	1	1	1	0	0
Arquet (78) -2	0		1		1		0	
Arquet (79) -3		0		0		1		0
Arquet (81) - 5	0		1		0		1	
Combe Grenat 1		1		1				
Combe Grenat 5	1		1		1			
Combe Grenat 10		1		1		1		
Combe Grenat 11	1		1		1			
Combe Grenat 27	1		1		1			
Grotte Boccard		1		1		1		1
La Chaise 1	1	1	1	1	1	1	0	0
La Chaise 12	1		1		1		0	
La Chaise 10		1		1		1		0
La Ferrassie 1	1	1	1	1				
La Quina H5		1						
Montgaudier		1		1		1		0
Monsempron 3		1		1		1		0
Moulay-Quercy								
M-D2-588	1		1		1		0	
M-D1-259		1		1		1		1
Moustier 1	1	1	1	1	1	1	0	0
	1	1	1	1	1	1	0	0
Regourdou	1	1	0	0	1	1	0	0
St Cesaire								
Mandible	1	1	1	1	1	1	0	0
maxi	1	1	1	1	1	1	0	0
Germany								
Ehringsdorf 6	1	1	1	1			0	0
Ehringsdorf G1	1	1	1	1	1	1	0	0
Ehringsdorf G2	1		1		1		0	
Ehringsdorf G3		1		1		1		1
Israel								
Amud	1	1	1	1	1	1	0	0
Kebara	1	1	1	1	1	1		
Tabun 2	0	0						
Italy								
Guattari Cave 3		1		1		1		0

Canines counting

canines	R/L	Mand	Max	Canine distal accessory ridge	Mesial ridge (Bushman canine)	canines	R/L	Mand	Max	Canine distal accessory ridge	Mesial ridge (Bushman canine)	canines	R/L	Mand	Max	Canine distal accessory ridge	Mesial ridge
Belgium						**France**						**Spain**					
Scladina						**Arcy sur Cure**						Cova Forada			1	0	1
Scia 4A-12	R	1		1	0	Arcy-C 6 nr 7	L	1		1		Gegant -5		1		1	0
Scia 4A-16	R		1	0	0	Arcy Bison p11.8			1	1	1	Las Palomas 35	L		1	0	1
Scia 4A-18	L		1	0	0	Combe Grenat 1		1		1	0	Las Palomas 74	R		1	1	0
Croatia						La Chaise 1	L	1		1	0	**Irak**					
Krapina D (Krapina 54)	L	1		0	0	La Ferrassie 1			1	0	1	Shanidar 1 mand	R/L	1		0	0
Krapina E (Krapina 55)	L	1		0	0	Monsempron 3	R		1	0	0	Shanidar 2 mand	R/L	1		1	0
Krapina E nr 49	L		1	1	1	**Moulay-Quercy**						**Uzbekistan**					
Krapina F nr 50	R		1	1	1	M-*-TNN2	L	1		1	0	Obi-Rakhmat			1	0	1
Krapina H (Krapina 58)	R/L	1		1	0	M-G4-144	L	1		1	0						
Krapina J (Krapina 59)	R/L	1		1	0	M-S-TNN1	R	1		1	0						
Krapina 147	L		1	1	1	M-I4-TNN3	R		1	0	0						
Krapina 146	L		1	1	0	**Moustier 1**	R	1		1	0						
Krapina 145	R	1		0	0		R		1	1	0						
Krapina 144	L		1	0	0	Regourdou		1		0	0						
Krapina 143	R	1		0	0	St Cesaire	R	1	1	0	1						
Krapina 142	L		1	0	1	**Germany**											
Krapina 141	R		1	0	0	Ehringsdorf 6 (F) (Weimar)		1		0	0						

Krapina 140 (Maxilla F)	R		1	0	0	Ehringsdorf G1		1		0	0
Krapina 139	L		1	0	0	**Israel**					
Krapina 138	L	1		0	0	Amud	L	0		0	0
Krapina 120	L	1		0	0	Amud	R		1	1	1
Krapina 119	L	1		0	0	Kebara	L	1		1	0
Krapina 76	R		1	0	0	Qafzeh 5			1	1	0
Krapina 75	R	1		0	0	Qafzeh 6			1	0	1
Krapina 59	R	1		0	0	Qafzeh 7			1	0	1
Krapina 56	R		1	0	0	Qafzeh 7		1		0	0
Krapina 37	L		1	0	0	Qafzeh 9		1		0	0
Krapina 36	R		1	0	0	Qafzeh 9			1	1	0
Vindija 206 Vi 206	R	1		0	0	**Italy**					
Vindija 287 Vi 287	R		1	0	0	Saccopastore 2			1	0	0
Vindija 288 Vi 288	L	1		0	0	Guattari Cave 3		1		1	0

Premolar counting

	P^3 Bifur. Ess.	P^3 acces.	P^3 access.	P^4 Bif. Ess.	P^4 -access.	P^4 acces. cusp	P^3 -ML Groove	P^3 -Transverse	P^3 -distal	P^3 -ling.	P^3 -ling.	P^4 - ML Groove	P^4 - "U" fissure	P^4 - "H" fissure	P^4 - "Y" fissure	P^4 - Tranverse	P^4 -distal	P^4 -ling.
Belgium																		
Scladina																		
Sclad 4A-1													0	0	1	1	1	1
Sclad 4A-2				1	1	1												
Sclad 4A-6							1	1	1	0	1							
Sclad 4A-9													0	0	1	1	1	1
Spy																		
Spy 1							0	1	1	1	1	1	0	1	0	1	1	1
Croatia																		
Mand D (KDP							1	1	1	0	1	1	0	0	1	1	1	1
Mand E (KDP							1	1	1	1	1	1	0	1	0	1	1	1
Mand F (KDP												1	0	0	1	1	1	1
Mand H (KDP							0	1	0	1	1	1	0	0	1	1	1	1
Mand J (KDP											1	1	0	1	0	1	1	1
Maxilla C(KDP				1	1	1												
Maxilla	1	1	1	1	1	1												
Maxilla E	1	1	0	1	1	1												
Maxilla	1	1	0	1	1	1												
Krapina 25							1	1	1	0	1							
Krapina 27																		
Krapina 30												0	0	0	1	1	1	1
Krapina 41				1	1	1												
krapina 26												1	1	0	0	1	1	1
Krapina 28							1	1	1	1	1							
Krapina 31												1	1	0	0	1	1	1
Krapina 38	1	1	1															
Krapina 47				1	1	1					1							
Krapina 29							1	1	1	1								
Krapina 32												1	1	0	0	1	1	1
Krapina 33							1	0	1	1	1							
Krapina 50												1	1	0	0	1	1	1
Krapina 34							1	1	0	1	1							
Krapina 35												1	1	0	0	1	1	1
Krapina 39	1	1	1															
Krapina 40				1	1	1												
Krapina 42				1	1	1												
Krapina 43	1	1	1															
Krapina 44				1	1	1												
Krapina 45	1	1	1															
Krapina 49				1	1	1												
Krapina 46				0	1	1												
Krapina 51																		
Krapina 52	1	1	1															
Krapina 53	1	1	1															
Krapina 54	1	1	1															
Krapina 111							1	1	1	1	1							
Krapina 113													0	0	1	1	1	1
Krapina 114							1	1	1	1	1							
Krapina 118												0	0	0	1	1	1	1
Czech																		
Kulna Max	1	1	1	1	1	1												
Ochoz mand							0	1	0	1	1	0	1	0	0	1	0	1

	P^3 Bifur. Ess.	P^3 acces.	P^3 access.	P^4 Bif. Ess.	P^4 -access.	P^4 acces. cusp	P^3 -ML Groove	P^3 -Transverse	P^3 -distal	P^3 -ling.	P^3 -ling.	P^4 - ML Groove	P^4 - "U" fissure	P^4 - "H" fissure	P^4 - "Y" fissure	P^4 - Tranverse	P^4 -distal	P^4 -ling.
France																		
Arcy Grotte du	1	1	1		1													
Arcy Grotte du	1	1	0		1	1												
Arcy Grotte du								1	1	1	1		0	0	1	1	1	1
Arquet no 7	1	1	1															
Arquet no 8				1	1	1												
Boccard gb77				1	0	0												
Combe Grenal												0	0	0	1	1	1	1
Combe Grenal								1	1	1	1							
Combe Grenal												1	0	0	1	1	1	1
La Chaise								1	1	1	0	1	1	0	0	1	1	1
BD 14 (I8-20)				1	1	0												
BD 9 (I8-3)							1											
La Quina 9								1	1	1	1		0	0	1		1	
La Quina 5		1	1		1	1												
Moulay-	0	0	0															
Moustier 1							1	1	1	1	1	0	0	0	1	0	1	1
Moustier 1 Max	1	1	1	1	1	1												
Petit Puymoyen								1	1	1	1	1	1	0	0	1	1	1
Petit Puymoyen							1	1	1	1	1							
Regourdou								1	1	1	1		0	0	1	1	1	1
St Cesaire							0	1	1	1	1	1	1	0	0	1	1	1
St Cesaire. Img	0	0	0	1	0	1												
Germany																		
Ehringsdorf G1												0	0	0	1	1	1	1
Israel																		
Amud							0	1	1	1	1	1	0	1	0	1	1	1
Kebara							0		1	1		0	0	1	0	1	1	1
Tabun C1							1	0	1	1	0	1	1	0	0	0	1	1
Italy																		
Fate 7	0	0	0															
Fate 8	1	1	0															
Guattari III							0	1	1	1	1							
Taddeo 2				1	1	0												
Saccospastore 2							0	1	1	1	0	0	1	0	0	1	1	1
Spain																		
Zafarraya uc							1	1	1	1	1							
Salt 2	0	1	0															
Salt 3				0	0	0												
Valdegoba VB1							1	1	0	1	1	0	0	0	1	1	1	1
Las Palomas 57												1	0	0	1	1	1	1
Las Palomas 59												0	1	0	0	1	1	1
Las Palomas 78												1	0	0	1	1	1	1
Las Palomas 87												1	0	0	1	1	1	1
Irak																		
Shanidar 2	0	1		0	0	0												
Shanidar 6 max	0	1	1	0	1													
Shanidar 6 man							0	1	0	1	1	0	1	0	0	1	0	1
Uzbekistan																		
Obi Rakmat upper third OR	0	1	0															
Obi Rakmat upper fourth				1	1	1												

M_1 counting

Sites	cusp 6	cusp 7	Deflecting wrinkle	X	y	+	Mid trigonid crest
Belgium							
Scladina							
Scia 4A-1	0	0	0	0	1	0	1
Scia 4A-9	0	0	0	0	1	0	1
Spy 1							
Spy 1	0	0					
Spy 2	0	0					
Croatia							
Krapina B (Krapina 52)	0	1	1	0	1	0	1
Krapina D (Krapina 54)	0	1	0	0	0	1	1
Krapina E (Krapina 55)	0	0	1	0	1	0	1
Krapina G (Krapina 57)	0	0	1	0	0	1	1
Krapina H (Krapina 58)	0	0	0	0	0	1	1
Krapina J (Krapina 59)	1	1	0	0	1	0	1
Krapina 82	0						1
Krapina 84	0	0					1
Krapina 81	0	0	0	0	1	0	0
Krapina 79	0	0	0				0
Krapina 77	0	0	1	0	1	0	0
Vindija 206 Vi 206				0	1	0	
Czech							
Ochoz	0	0		1	0	0	1
Germany							
Ehringsdorf G1	1	1	1	0	1	0	1
Ehringsdorf I	0	0	0	0	1	0	1
Israel							
Kebara	0	0	0				1
Tabun C1	1	0	1	0	1	0	1
Tabun C7	0	0		0	1	0	1
Italy							
Taddeo 4	1	0	1	0	1	0	1
Guattari Cave 3				0	1	0	
Fate 2	0	0	1	1	1	0	1
Fate 6	0	0	0	0	1	0	1

Sites	cusp 6	cusp 7	Deflecting wrinkle	X	y	+	Mid trigonid crest
France							
Arcy-M1 8-1 nr 30	1	0	1	0	1	0	1
Arcy-M1 8-3 nr 35	0	0	0	0	1		1
Arcy sur cure 1955-5-1	0	0					
Arcy sur cure 1977-2-8	0	0		1	0	0	0
Combe Grenat 1	1	0	1	0	1	0	1
Combe Grenat 4	0	0	0	0	1	0	0
Genay 3	1	1	0	0	1	0	0
La Chaise 1	0	0	0	0	1	0	1
La Chaise BDJ4C9	1	1	1	0	1		1
La Ferrassie 8	1	1	0				
La Quina H5 nr 35	1	1	0	0	1		1
La Quina H9 nr 1	1	1	1	0	1		0
Montgaudier				0	1	0	
Moulay-Quercy							
M-G2-419	0	0	0	1	0	0	1
M-D1-230	0	0	0	0	1		1
M-L4-TNN5	0	0	0	1	0	0	1
Moustier 1	1	0	0	1	0	0	1
Petit Puymoyen PPm I	0	1	0	1	0	0	1
Petit Puymoyen PPm III	0	0	0	0	1	0	0
Regourdou	0	0	0	0	1	0	1
Rochelot	0		0				
St Cesaire Mand.	0	0	0	0	1	0	0
Vergisson M1	0	0	0	0	0	1	1
Spain							
Banyolas	0	0		0	1	0	0
cova del Gegant -5	0	0	1	0	1	0	1
Las Palomas SP 59 M1	0	0	0	0	1	0	1
Las Palomas SP 84	0	0	0	0	1	0	0
Los Mor Gabasa Ga1.Rev	0	0					
Gibraltar Devil's Tower	1	0	0	0	1	0	0
Valdegoba V1	1	1		0	1	0	1
Iraq							
Shanidar 1	0	0					1
Shanidar 2	1	0	0	0	1	0	0
Shanidar 4				0	1	0	
Shanidae 6				0	1	0	

M_2 counting

Sites	cusp 6	cusp 7	Deflecting wrinkle	X	y	+	Distal trigonid crest	Mid trigonid crest
Belgium								
Scladina								
Scia 4A-1 /M2	0	0	0	0	1	0	1	1
Scia 4A-9/M2	0	0	0	0	1	0	1	1
Spy 1	0	0	0				0	0
Croatia								
Krapina D (Krapina 54)	1	0	0	0	1	0	0	1
Krapina E (Krapina 55)	1	0	1	0	0	1	0	0
Krapina G (Krapina 57)	0	0	0	0	0	1	0	1
Krapina H (Krapina 58)	0	0	0	0	0	1	0	1
Krapina J (Krapina 59)	0	0	0	0	1	0	0	1
Krapina 107	1	0	0	0	0	1	0	1
Krapina 86	1	0	0	0	0	1	0	1
Krapina 80	0	0	0	0	0	1	0	1
Krapina 10	1	1	0	0	0	1	0	1
Krapina 6	0	0	0	0	0	1	0	1
Krapina 3	0	0	0	0	0	1	0	1
Krapina 2	0	0	0	0	0	1	0	1
Krapina 1	0	0	0	0	1	0	0	0
Vindija 206 Vi 206	0	0	0	0	1	1	0	1
Vindija 231 Vi 231				0	1	0		
Czech								
Ochoz	0	0	0	1	0	0	0	0
France								
Arcy-M2 8-2 nr 21 Renne	1	1	0	1	0	0	0	1
Arcy-M2 8-4 nr 5 Renne	1	0	0	0	1	0	0	1
Arcy sur cure Hye 1977-2-8	0	0	0	0	1	0	0	0
Arcy-M2 8-4 nr 16 Renne	0	0						
Grotte Boccard	0	0	0	0	0	1	0	0
La Chaise 1	0	0	0	0	0	1	0	1
La Quina H5 nr 35	0	0	0	0	1	0	0	1
La Quina H9 nr 1	0	0	0	0	1	0	0	1
Moulay-Quercy								
M-G2-419	0	0	0	0	0	1	0	1
Moustier 1	1	1	1	0	1	0	0	1
Petit Puymoyen PPm I	0	0	0	0	1	0	0	1
Petit Puymoyen PPm IV	0	0	0	1	0	0	0	1
Petit Puymoyen PPm V	1	1	1	0	0	1	0	1
Regourdou	0	0	0	0	0	1	0	1
St Cesaire	0	0	0	0	1	0	0	1

Sites	cusp 6	cusp 7	Deflecting wrinkle	X	y	+	Distal trigonid crest	Mid trigonid crest
Germany								
Ehringsdorf 6 (F)	0	0					0	1
Ehringsdorf G1	0	0	1	0	0	1	0	1
Israel								
Amud	0	0		1	0	0	0	1
Kebara	0	0	1	0	0	1	0	1
Tabun C	0	0					0	1
Tabun C7	0	0		0	1	0		1
Italy								
Guattari Cave 3	0	0	1	0	1	0	0	1
Fate 2	0	0					0	1
Fate 5	0	0	0	0	1	0		0
Fate 12	0	0					0	1
Pologne								
Stajnia S4300	1	0	0	0	1	0	0	1
Spain								
Banyolas	0	0						
Las Palomas 29	0	0	0	0	1	0	0	1
Las Palomas 80	0	0	0	0	1	0	0	0
Las Palomas SP 59 M2	0	0	0	0	1	0	0	1
Valdegoba V1	1	1		0	1	0	1	1
Iraq								
Shanidar 1	0	0		0	1	0		
Shanidar 2	0	0		0	1	0	0	1
Shanidar 6				0	1	0		

M_3 counting

M_3	cusp 6	cusp 7	Deflecting wrinkle	X	y	+	Mid trigonid crest
Belgium							
Scia 4A-1	1	0	0	0	0	1	1
Croatia							
Krapina D (Krapina 54)	1	0	0	0	0	1	1
Krapina G (Krapina 57)	0	0	1	0	1	0	1
Krapina H (Krapina 58)	0	0	0	0	0	1	1
Krapina J (Krapina 59)	0	0	0	0	0	1	1
Krapina 85	1	0	1	0	1	0	0
Krapina 9	0	0	0	1	0	0	1
Krapina 8	0	0	0	0	0	1	1
Krapina 7	0	0	1	1	0	0	1
Krapina 5	0	0	0	0	0	1	1
Krapina 4	0	0		0			1
Vindija 206 Vi 206	0	0	0	1	0	0	0
Vindija 231 Vi 231	0	0		1	0	0	1
Czech							
Ochoz	0	0		1	0	0	1
France							
Combe Grenat 12	0	0	0	1	0	0	1
La Chaise 1	1	0	0	0	0	1	1
La Quina H5 nr 35	0	0	0	0	1	0	1
La Quina H9 nr 1	1	0	0	0	0	1	0
Moulay-Quercy							
M-G2-419	0	0	0	0	1	0	1
Moustier 1			1	0	0	1	1
Petit Puymoyen PPm V	0	0	0	0	0	1	0
Regourdou	0	0	0	0	0	1	1
St Cesaire	1	0	0	0	0	1	1
Germany							
Ehringsdorf 6 (F)							1
Hunas 1	1	0	0	0	1	0	1
Greece							
Lakonis	1		0				1
Israel							
Amud	1	1					0
Kebara	0	0		0	1	0	1
Tabun C1							0
Tabun C7	0	0		1	0	0	1
Italy							
Guattari Cave 2	0	0		0	0	1	
Guattari Cave 3	0	0		0	1	0	
Fate 3	0	0	0	0	0	1	1

Spain							
Banyolas	0	0	0	1	0	0	0
Irak							
Shanidar 1	0	0	0	0	1	0	1
Shanidar 2	0	0	0	0	1	0	1

M^1 counting

Sites	M^1-C4	M^1-C5	M^1-Ca
Belgium			
Scla 4A-4	1	1	0
Spy 1 Spy 11c			1
Croatia			
Maxilla A (KDP 1)	1	1	1
Maxilla B (KDP 2)	1	1	1
Maxilla C (KDP 3)	1	1	1
Maxilla D (KDP 4)	1	1	1
Maxilla F (KDP 6)	1	1	0
Krapina 100 (KDP 22)	1	1	1
Krapina 134 (KDP 3)	1	0	1
Krapina 136 (KDP 23)	1	0	0
Krapina 161 (KDP 1)			1
Krapina 164 (KDP 6)		0	0
Krapina 167 (KDP 19)	1	0	0
Krapina 171 (KDP 4)	1	0	0
Krapina 174 (KDP 1)	1	0	0
Czech			
Kulna	1	0	0
France			
Arcy-M1 Grotte du Bison	1	1	0
Arcy-M1 Grotte du Renne	1	0	0
Combe Grenal 13	1	0	1
La Chaise 8	1	0	0
La Quina 18	1	1	1
La Quina 5	1	0	0
Moulay-Quercy			
M-I4-55	1	1	0
Moustier 1	1	1	1
Petit Puymoyen PPm 2	1	0	0
St Cesaire	1	0	0

Sites	M^1-C4	M^1-C5	M^1-Ca
Italy			
Taddeo 3	1	0	1
Fate 13	1	0	0
Saccopastore 1	1	0	0
Saccopastore 2	1	0	0
Pologne			
Stajnia S4619	1	1	1
Spain			
Cova Forada CF-1	1	0	0
El Salt 4	1	0	0
Cova Negra CN 42175	1	0	0
Iraq			
Shanidar 1	1	0	0
Shanidar 2	1	0	0
Shanidar 5	1		
Shanidar 6	1	0	0

M^2 counting

Sites	M^2-C4	M^2-C5	M^2-Ca
Belgium			
Scla 4A-3	1	1	1
Spy 1 Spy 11D			1
Croatia			
Maxilla C (KDP 3)	1	1	0
Maxilla D (KDP 4)	1	1	0
Maxilla F (KDP 6)	1	0	0
Krapina 58 (KDP 32)	1	0	0
Krapina 96	1	0	1
Krapina 98	1	0	1
Krapina 101	1	0	0
Krapina 135 (KDP 23)	1	0	0
Krapina 165 (KDP 4)	1	0	0
Krapina 166 (KDP 32)	1	0	0
Krapina 169 (KDP 19)	1	0	0
Krapina 172 (KDP 25)	1	0	0
Krapina 175 (KDP 25)	1	0	0
Krapina 176 (KDP 24)	1	0	0
Krapina 177 (KDP 33)	1	0	0
Krapina 192 (KDP 2)	1	0	0
Vi259	1	1	0
France			
Arcy-M2 Grotte du Bison	1	0	0
Combe Grenal 9	1	0	1
La Chaise 8	1	0	0
La Quina 5	1	0	0
La Quina 20 a	1	0	0
La Quina 22	1	0	0
Moulay-Quercy			
M-G2-117	1	0	0
M-F3-215	1	0	0
Moustier 1	1	1	0
Petit Puymoyen PPm 2	1	0	0
St Cesaire	1	0	0
Germany			
Feldhofer NN16	1	1	0
Feldhofer NN31	1	0	0
Italy			
Saccopastore 1	1	1	0
saccopastore 2	1	1	0
Pologne			
Stajnia S5000	1	0	0
Spain			
Las Palomas SP36	1	0	0
Irak			
Shanidar 1	1	0	0
Shanidar 2	1	0	0
Shanidae 6	1	0	0

M^3 counting

Sites	M^3-C4	M^3-C5	M^3-Ca
Belgium			
Scladina			
Scla 4A-8	1	1	1
Spy 1			
Spy 1 Spy 583a on Spy 11b	1		
Spy 1 Spy 94a			
Spy 2 Spy 578f on Spy 2A	1		
Croatia			
Krapina 97	1	0	0
Krapina 137 (KDP 24)	1	0	0
Krapina 162 (KDP 25)	1	0	0
Krapina 163 (KDP 4)	1	0	0
Krapina 170 (KDP 19)	1	0	0
Krapina 173			
Krapina 178 (KDP 33)	1	0	0
Krapina 179 (KDP 24)	1	0	0
Krapina 180 (KDP 24)	1	0	0
France			
Arcy-M3 Grotte du Bison	0	0	0
La Chaise 8	1	0	0
La Quina 5	0		
La Quina 20b	0		
Moustier 1	1	1	0
Petit Puymoyen PPm 2	1	0	0
St Cesaire	1	0	0
Germany			
Feldhofer NN33	1	0	0
Italy			
Saccopastore 1	0	0	0
Saccopastore 2	0	0	0
Irak			
Shanidar 1	1	0	0
Shanidar 2	1	0	0
Shanidar 3	1	0	0
Shanidar 5	1	0	0
Shanidar 6	1	0	0

Freq.- Nbr Incisor to Premolar

Sites	**I1 convexity**	I2	**I1 shoveling**	I2	**I1 Lingual**	I2	**I1**	I2	**Canine distal**	**P_3-ML Groove**	**P_3-Transverse**	**P_3-distal**	**P_3-ling.**	**P_3-ling.**	**P_4- ML**	**P_4- "U"**	**P_4- "H"**	**P_4- "Y"**	**P_4- Tranverse**	**P_4-distal**	**P_4-ling.**
Croatia																					
freq.	7	9	7	9	3	1	0	1	2	9	9	8	8	11	10	5	2	6	13	13	13
Nbr	7	9	7	9	6	5	6	8	13	10	10	10	10	11	12	13	13	13	13	13	13
France																					
freq.	6	9	6	8	5	8	1	0	7	3	9	9	9	8	4	3	0	6	7	9	8
Nbr	7	10	7	10	6	8	6	8	9	4	9	9	9	9	6	9	9	9	8	9	8
Belgium																					
freq.	1	1	1	1	1	1	1	1	1	1	2	2	1	2	1	0	0	2	3	3	3
Nbr	1	1	1	1	1	1	1	1	1	2	2	2	2	2	3	3	3	3	3	3	3
Czech																					
freq.	2	1	1	0	1	1	0	0		0	1	0	1	1	0	1	0	0	1	0	1
Nbr	2	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1
Germany																					
freq.	2	2	2	2	1	1	0	0	0						0	0	0	1	1	1	1
Nbr	2	2	2	2	1	1	2	2	2						1	1	1	1	1	1	1
Greece																					
freq.																					
Nbr																					
Israel																					
freq.	1	1	1	1	1	1			1	1	1	3	3	1	2	1	2	0	2	3	3
Nbr	2	2	1	1	1	1			2	3	2	3	3	2	3	3	3	3	3	3	3
Poland																					
freq.																					
Nbr																					
Italy																					
freq.		1		1		1		0	1	0	1	1	0								
Nbr		1		1		1		1	1	*2*	*2*	*2*	*2*								
Spain																					
freq.									1	2	2	1	2	2	3	1	0	4	5	5	5
Nbr									1	2	2	2	2	2	5	5	5	5	5	5	5
Iraq																					
freq.									1	0	1	0	1	1	0	1	0	0	1	0	1
Nbr									2	1	1	1	1	1	1	1	1	1	1	1	1

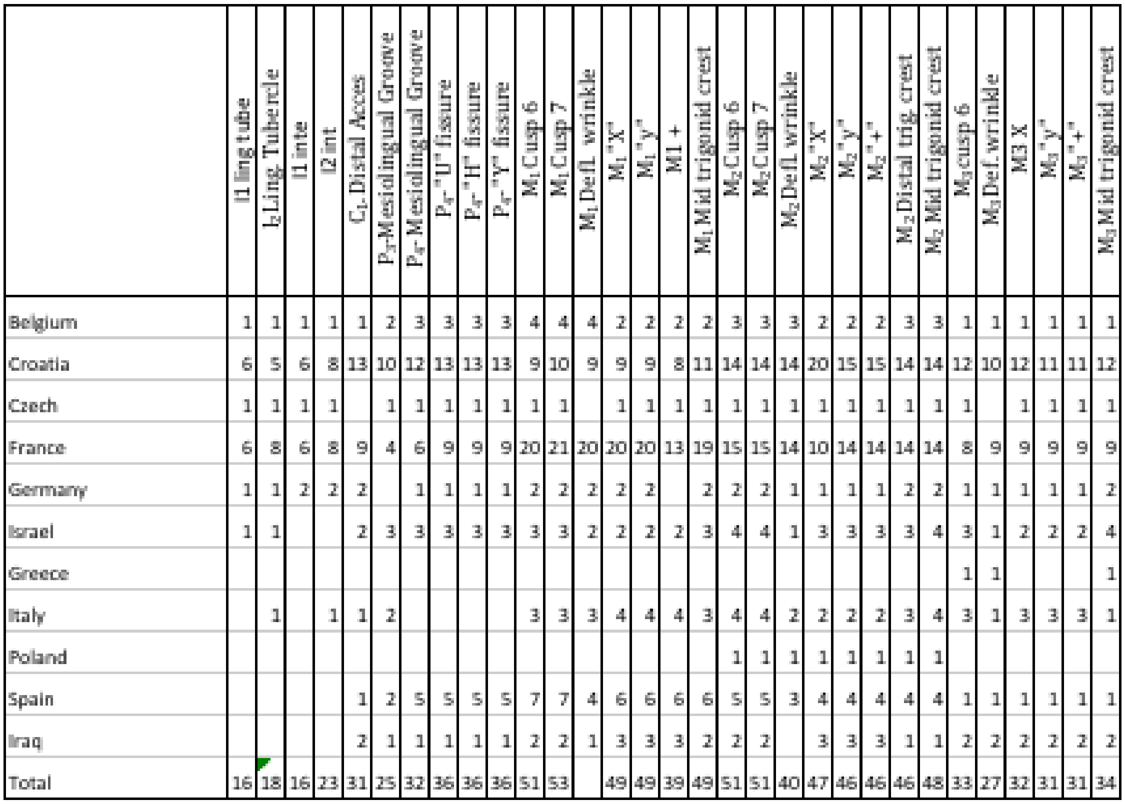
Freq.- Nbr Molar

	M_1 cusp 6	M_1 cusp 7	M_1 Defl. wrinkle	M_1X	M_1y	M_1+	M_1 Mid trigonid crest	M_2 cusp 6	M_2 cusp 7	M_2 Deflecting wrinkle	M_2X	M_2y	M_2+	M_2 Distal trigonid crest	M_2 Mid trigonid crest	M_3 cusp 6	M_3 cusp 7	M_3 Deflecting wrinkle	M_3 X	M_3 y	M_3 +	M_3 mid trigonid crest
Croatia																						
freq.	1	3	4	0	6	3	8	5	1	1		5	11	0	12	2	0	3	4	2	5	10
Nbr	11	10	9	9	9	8	11	14	14	14	20	15	15	14	14	12	12	10	12	11	11	12
France																						
freq.	8	6	4	5	14	1	13	4	3	2	2	7	5	0	12	3	0	1	1	2	6	7
Nbr	22	21	20	20	20	13	19	15	15	14	10	14	14	14	14	8	8	9	9	9	9	9
Belgium																						
freq.	0	0	0	0	2	0	2	0	0	0	0	2	0	2	2	1	0	0	0	0	1	1
Nbr	4	4	2	2	2	2	2	3	3	3	2	2	2	3	3	1	1	1	1	1	1	1
Czech																						
freq.	0	0		1	0	0	1	0	0	0	1	0	0	0	0	0	0		1	0	0	1
Nbr	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1
Germany																						
freq.	1	1	1	0	2		2	0	0	1	0	0	1	0	2	1	0	0	0	1	0	2
Nbr	2	2	2	2	2		2	2	2	1	1	1	1	2	2	1	1	1	1	1	1	2
Greece																						
freq.																1		0				1
Nbr																1		1				1
Israel																						
freq.	1	0	1	0	2	0	3	0	0	1	1	1	1	0	4	1	1	0	1	1	0	2
Nbr	3	3	2	2	2	2	3	4	4	1	3	3	3	3	4	3	3	1	2	2	2	4
Poland																						
freq.								1	0	0	0	1	0	0	1							
Nbr								1	1	1	1	1	1	1	1							
Italy																						
freq.	1	0	2	1	4	0	3	0	0	1	0	2	0	0	3	0	0	0	0	1	2	1
Nbr	3	3	3	4	4	4	3	4	4	2	2	2	2	3	4	3	3	1	3	3	3	1
Spain																						
freq.	2	1	1	0	6	0	3	1	1	0	0	4	0	1	3	0	0	0	1	0	0	0
Nbr	7	7	4	6	6	6	6	5	5	3	4	4	4	4	4	1	1	1	1	1	1	1
Iraq																						
freq.	1	0	0	0	3	0	1	0	0		0	3	0	0	1	0	0	0	0	2	0	2
Nbr	2	2	1	3	3	3	2	2	2		3	3	3	1	1	2	2	2	2	2	2	2

Freq. – Nbr Maxillary

	I^1 convexity	I^2	I^1 shoveling	I^2	I^1 Lingual Tubercle	I^2	I^1 Interruption groove	I^2	C^1 distal accessory ridge	C^1 Mesial ridge	P^3 Bifur. Ess. crest buc./ ling.	P^3 acces. ridge mes. /dist.	P^3 access. cusp mes./ dist.	P^4 Bif. Ess. crest buc./ ling.	P^4-access. ridge mes./ dist.	P^4 acces. cusp mes./ dist.	M^1 -C4	M^1 -C5	M^1 Ca	M^2-C4	M^2-C5	M^2-Ca	M^3-C4	M^3-C5	M^3-Ca
Belgium																									
Event									0	0				1	1	1	1	1	1	1	1	2	3	1	1
# of teeth									2	2				1	1	1	1	1	2	1	1	2	3	1	1
Croatia																									
Event	14	15	14	15	13	13	5	6	4	4	10	10	8	10	11	11	12	6	6	17	3	2	8	0	0
Nbr of teeth	14	15	14	15	13	13	11	11	14	14	10	10	10	11	11	11	12	12	12	17	17	17	8	8	8
Czech																									
Event											1	1	1	1	1	1	1	0	0						
Nbr of teeth											1	1	1	1	1	1	1	1	1						
France																									
Event	8	12	9	11	0	0	8	9	0	3	3	1	4	4	0	5	6	5	10	3	0	12	1	1	4
Nbr of teeth	9	12	9	11	9	11	8	9	5	9	6	2	6	7	2	5	8	7	10	10	10	12	12	12	7
Germany																									
Event	1	1	1	1	0	0	1	1	0	1												2	1	0	1
Nbr of teeth	1	1	1	1	1	1	1	1	1	1												2	1	1	1
Israel																									
Event	1	1	1	1	1	1	0	0	1	1															
Nbr of teeth	1	1	1	1	1	1	1	1	1	1															
Italy																									
Event									0	0	1	1	0	1	1	0	4	0	1	2	2	0	0	0	0
Nbr of teeth									1	1	2	2	2	1	1	1	4	4	4	2	2	2	2	2	2

Number of comparison low teeth



	I1 ling tube	I_2 Ling. Tubercle	I1 inte	I2 int	C_1. Distal Acces	P_3-Mesiolingual Groove	P_4- Mesiolingual Groove	P_4-"U" fissure	P_4-"H" fissure	P_4-"Y" fissure	M_1 Cusp 6	M_1 Cusp 7	M_1 Defl. wrinkle	M_1 "X"	M_1 "y"	M1 +	M_1 Mid trigonid crest	M_2 Cusp 6	M_2 Cusp 7	M_2 Defl. wrinkle	M_2 "X"	M_2 "y"	M_2 "+"	M_2 Distal trig. crest	M_2 Mid trigonid crest	M_3 cusp 6	M_3 Def. wrinkle	M3 X	M_3 "y"	M_3 "+"	M_3 Mid trigonid crest
Belgium	1	1	1	1	1	2	3	3	3	3	4	4	4	2	2	2	2	3	3	3	2	2	2	3	3	1	1	1	1	1	1
Croatia	6	5	6	8	13	10	12	13	13	13	9	10	9	9	9	8	11	14	14	14	20	15	15	14	14	12	10	12	11	11	12
Czech	1	1	1	1		1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1
France	6	8	6	8	9	4	6	9	9	9	20	21	20	20	20	13	19	15	15	14	10	14	14	14	14	8	9	9	9	9	9
Germany	1	1	2	2	2		1	1	1	1	2	2	2	2	2		2	2	2	1	1	1	1	2	2	1	1	1	1	1	2
Israel	1	1			2	3	3	3	3	3	3	3	2	2	2	2	3	4	4	1	3	3	3	3	4	3	1	2	2	2	4
Greece																										1	1				1
Italy		1		1	1	2					3	3	3	4	4	4	3	4	4	2	2	2	2	3	4	3	1	3	3	3	1
Poland																		1	1	1	1	1	1	1	1						
Spain					1	2	5	5	5	5	7	7	4	6	6	6	6	5	5	3	4	4	4	4	4	1	1	1	1	1	1
Iraq					2	1	1	1	1	1	2	2	1	3	3	3	2	2	2		3	3	3	1	1	2	2	2	2	2	2
Total	16	18	16	23	31	25	32	36	36	36	51	53		49	49	39	49	51	51	40	47	46	46	46	48	33	27	32	31	31	34

Number of comparison upper teeth

	I^2 Inter. groove	C^1 distal acce. ridge	C^1 Mesial ridge)	P^3 Bifur. Ess. crest buc./ lin	P^3 acces. ridge mes. /dist.	P^3 access. cusp mes./ dist.	P^4 Bif. Ess. crest buc./ ling	P^4-access. ridge mes./ dist.	P^4 acces. cusp mes./ dist.	M^1-Cusp 4	M^1-Cusp 5	M^1-Carabelli	M^2-Cusp 5	M^2 Carabelli	M^3-Cusp 4	M^{3}cusp 5
Belgium		2	2				1	1	1	1	1	1	1	2	3	1
Croatia	11	14	14	10	10	10	11	11	11	12	12	12	17	17	8	8
Czech				1	1	1	1	1	1	1	1	1				
France	9	5	9	6	2	6	7	2	5	8	7	10	10	12	12	12
Germany	1	1	1											2	1	1
Israel	1	1	1													
Greece																
Italy		1	1	2	2	2	1	1	1	4	4	4		2	2	2
Poland																
Spain																
Iraq																
Total	22	24	28	19	15	19	21	16	19	26	25	28	28	35	26	24