NEANDERTAL DENTAL MORPHOLOGY:

IMPLICATIONS FOR MODERN HUMAN ORIGINS

by

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IMPLICATIONS FOR MODERN HUMAN ORIGINS

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ABSTRACT

Research on Neandertal dentitions has been limited primarily to simple dental metrics, dental proportions and a few dental traits that seem to distinguish these from anatomically modern *Homo sapiens* (e.g., derived incisor morphology and taurodont molars). Consequently, Neandertal postcanine dental morphology has been generally assumed to be much like our own. This research examines this assumption through a systematic and comparative study of Neandertal postcanine dental morphology. Results are interpreted in light of two competing models for modern human origins: Multiregional Evolution (MRE) and Recent African Origin (RAO).

Postcanine dental data were collected using the well-standardized methodology of the Arizona State University dental anthropology system. Additional dental traits were added by the author. Samples include individuals representing *Homo erectus*, archaic *Homo sapiens*, Neandertals, early anatomically modern *Homo sapiens*, Upper Paleolithic Europeans and seven recent human geographic populations. Univariate and multivariate statistical analyses, together with cladistic analysis, were used to make quantified assessments of Neandertal affinities.

The results are inconsistent with predictions of the Multiregional Evolution hypothesis as it concerns Europe: phenetic analyses indicate that contemporary and Upper Paleolithic Europeans are among the groups *least similar* to Neandertals, and that there is no evidence of gradual evolution toward the modern human dental condition in Europe. In addition, Neandertals were found to exhibit a number of dental traits whose frequencies and combination of occurrence should be considered uniquely derived in

their lineage. The results of the cladistic analysis are inconsistent with the phylogenetic hypothesis that Neandertals and amHs share a recent common ancestor that is unique to them. Instead, the data are consistent with a hypothesis that archaic *Homo sapiens* and Neandertals share a more recent common ancestor with each other then either does with anatomically modern *Homo sapiens*. Finally, the complete lack of derived Neandertal dental traits in Upper Paleolithic Europeans is difficult to reconcile with hypotheses of intensive gene flow between Neandertals and Upper Paleolithic Europeans.

The fact that Upper Paleolithic Europeans and early amHs are phenetically similar, together with the fact that Upper Paleolithic Europeans are less similar to recent Europeans than to some other recent groups, likely indicates that the modern European dental pattern was acquired relatively recently.

Finally, the overall phenetic similarity and evidence for dental synapomorphies between Neandertals and European archaic *Homo sapiens* conform to the hypothesis that European archaic *Homo sapiens* is best interpreted as an early representative of the Neandertal lineage.

For my father and mother,

C. David Bailey

and

Frieda B. Bailey

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INTRODUCTION

> "The decisive factors in each attempt at tracing the line of human evolution are found in paleontological evidence. Nowhere can it be demonstrated as clearly as in the dentition" (Weidenreich, 1937:2).

Overview

The origin of modern humans has been debated for decades without resolution. One of the key issues in this debate is the question of the ancestral relationship between Neandertals and anatomically modern *Homo sapiens* (amHs). Neandertals have been the focus of debate since their remains were identified in Feldhofer Cave, Germany in 1856 (Spencer, 1984; Trinkaus and Shipman, 1993). Yet, after more than a century of intensive study, there is little agreement regarding their taxonomic status and phylogenetic role in human evolution.

Studies of Neandertal morphology have traditionally focused on their distinctive cranial and postcranial features (Boule and Vallois, 1957; Franciscus, 1999; Holliday, 1997; Howells, 1975; Hublin, 1978; Le Gros Clark, 1964; Rak, 1986; Santa Luca, 1978; Stringer and Gamble, 1993; Stringer et al., 1984; Trinkaus, 1981). More recently, studies have indicated that Neandertals also exhibit a suite of distinct dental morphological features (Bailey, 2000b; 2001; Bailey and Turner, 1999; Crummett, 1994; Smith, 1989; Tattersall and Schwartz, 1999; Tillier et al., 1989) and dental proportions (Stephan and Trinkaus, 1998). Whether or not dental morphological traits can make a contribution to understanding Neandertal phylogeny was debated in the first half of the last century (e.g., Boule, 1923; Boule and Vallois, 1957; Keith, 1924; 1925; Krogman, 1927; Patte, 1959; Weidenreich, 1937). However, descriptive studies of particular fossils

rather than systematic, comparative studies have since dominated the literature on the teeth of these and other Late Pleistocene hominids (e.g., Genet-Varcin, 1966; 1972; Smith, 1976; Tillier, 1979; 1991; 1989; Trinkaus, 1978b; 1978c; Trinkaus et al., 2000; Wolpoff, 1979).

Since Étienne Patte's 1953 monograph, a comprehensive comparative study of Neandertal dentition has not been undertaken. In the past 50 years many more fossils have been discovered. In addition, systematized scoring systems – like the Arizona State University dental anthropology system (ASUDAS) – that facilitate comparative study have been developed. Although tooth crown morphology has played an important role in debates over the phylogeny of Plio-Pleistocene hominids (see Grine, 1985; 1990; Suwa et al., 1994; Wood et al., 1983; Wood and Uytterschaut, 1987), the same approach — systematizing a large set of dental morphological characters — has not yet been applied to evolutionary relationships among Middle and Late Pleistocene hominids. As a result, little is known about the variability and temporal change in dental morphology during this important time period.

The debate over modern human origins

Over the past two decades, research on modern human origins has focused on interpreting fossil remains within the framework of two competing models: Multi-Regional Evolution (MRE: Frayer et al., 1993; Wolpoff et al., 1984) and Recent African Origin (RAO, also "Out of Africa" or "Eve Theory" Cann, 1987; Stringer and Andrews, 1988; Stringer et al., 1984). The RAO model developed out of Howells'(1976) idea of a single and recent origin for amHs (the Noah's Ark model). Advocates of the RAO

model posit a monocentric origin for amHs that most likely took place in Africa or the Near East about 100,000 years ago. According to the RAO model, amHs subsequently spread and replaced existing archaic humans in the rest of the Old World. While some advocates of this model do not rule out the possibility that incoming modern groups and pre-existing archaic humans may have intermixed during the replacement process, they contend that any admixture that did occur was insignificant in explaining the emergence of modern human morphology (Stringer and Bräuer, 1994:417).

Weidenreich (1943) and Coon (1948) proposed that the evolutionary pathway to modern humans was through Multiregional Evolution. As the name implies, this was a polycentric model that proposed that the transition to amHs took place in many parts of the Old World. This version of MRE, which advocated relatively independent evolution of modern geographic populations, failed to explain why these separate groups did not evolve into separate species. Later advocates of MRE have elaborated upon and revised this theory over the past two decades (Frayer et al., 1993; Wolpoff et al., 1984). The more recent manifestation of MRE hypothesizes that gene flow kept geographically distinct populations from differentiating into distinct species while local selection for certain features (and drift for others) maintained inter-regional variation (Frayer et al., 1993). Under this model, certain 'modern' features evolved in different geographical regions and subsequently spread to other regions through a network of interconnected populations. In this way, all archaic populations would have shared a common evolutionary trajectory (Smith et al., 1989; Wolpoff et al., 1994). Not surprisingly,

advocates for MRE believe that pre-existing archaic humans in a particular region contributed significantly to later human evolution in that region.

Offering a twist on the traditional "replacement" hypothesis, Turner's (1995) Shifting Continuity model suggests that modern humans dispersed from Southeast Asia around 50,000 years ago and replaced modern humans in Africa, Europe and North Asia. According to Turner (1987; 1990a) this thesis is supported by the finding that Southeast Asians have the least specialized dental pattern (Sundadonty) of all living humans (i.e., being neither especially complex nor especially simplified). This, he claims, makes Southeast Asia a better candidate for the source of modern humans because it is easier to derive other regional patterns from Sundadonty than it is to derive them from more complex patterns of, say, Africans, or the more simplified pattern of Europeans.

While, even recently, the debate on modern human origins has focused on MRE or RAO hypotheses (e.g., Holliday, 1999; Kidder, 1999; Wolpoff et al., 1999), many paleoanthropologists who study Late Pleistocene human evolution no longer view these models as mutually exclusive. Instead, there has been a tendency for researchers to accept some variation of RAO (e.g., Weak Garden of Eden hypothesis of Harpending et al., [1993] or Multiple Dispersals of Lahr and Foley [1998]) or some form of "RAO with admixture" hypothesis. Smith (1984; Smith et al., 1989; Smith and Spencer, 1984) and Bräuer (1984; 1989; 1992) have formally outlined hypotheses that combine aspects of RAO and MRE. The primary difference between these intermediate models is whether Neandertals are viewed as contributing significantly (Assimilation model of Smith et al. [1989]) or minimally (Afro-European *sapiens* model of Bräuer [1984]) to the amHs gene

pool. Evidence of *in situ* development of certain "modern" morphology in Central Europe (Smith, 1982) and of possible hybridization between Neandertals and amHs (Duarte et al., 1999) have been cited in support of these intermediate models.

Although an "Recent African Origin with admixture" model may be the most appropriate for conceptualizing modern human origins, the extent of admixture has not been specified. Relethford (1995) has suggested that, over the long-term, African population size may have been three times that of populations elsewhere. He has demonstrated that if we accept these population size discrepancies, the African population would have the greatest genetic effect on later human evolution. Thus, we might expect contemporary modern humans across the Old World to more closely resemble earlier populations in Africa even in the face of gene flow between local regions (Relethford, 1999:9). Relethford and Jorde (1999a) have also suggested that a demonstration of continuity in just one region outside Africa would render Multiregional continuity a valid theory. This is significant because Wolpoff has recently argued that admixture and regional continuity are one in the same (Wolpoff, 1995b), and that demonstration of regional continuity of only a few characters is sufficient for disproving complete replacement (pers. comm., 2000).

The Neandertal problem

Historically, Neandertals have played a central role in the debate over modern human origins. During the early and middle part of the last century hypotheses about their relationship to modern humans were interpreted according to three schools of thought (Spencer, 1984; Trinkaus and Shipman, 1993). One group hypothesized that

human evolution across the Old World went through a Neandertal phase of development (Hrdlička, 1911; Weidenreich, 1943). According to this scheme, European Neandertals would have evolved directly into modern Europeans. Others believed that a more generalized, pre-Neandertal hominid gave rise to both modern humans and "classic" Neandertals and that the latter group became extinct, perhaps through overspecialization (Howell, 1951; Sergi, 1958). Finally, there were those who argued that *Homo sapiens* had a long evolutionary history that did not include Neandertals at all (Boule, 1923; Vallois, 1958). This "pre-*sapiens* theory" was largely based on questionably ancient fossils with modern morphology (e.g., Piltdown), and it gradually lost support with new dating techniques and new fossil discoveries. The other two theories (Neandertal Phase and the pre-Neandertal) have been subsumed into the two competing models that are still debated today.

The "Neandertal problem" continues to be a point of contention between supporters of RAO and MRE. Although many paleoanthropologists who study modern human origins are moving toward accepting some form of the "RAO with admixture" model, their views differ regarding the magnitude of this admixture. That is, whether the Neandertal genetic contribution to amHs was minimal and the hybridization period brief, such that the "transition" to modern humans approximated a replacement event; or, whether Neandertal genetic contribution to the amHs gene pool was considerable and the period of hybridization gradual (Stringer, 2001). Whether or not RAO supporters conclude that Neandertals belong in their own species (*Homo neanderthalensis*: [Rak, 1986; Schwartz and Tattersall, 1996; Stringer, 1996]), they do not believe they

contributed significantly to the evolution of amHs (Stringer and Bräuer, 1994). Alternatively, MRE supporters view Neandertals as a racial variant of *Homo sapiens* (Clark, 1992; Wolpoff et al., 1994), allowing that Neandertals may have played a significant role in amHs evolution. These different views affect how the fossil record is interpreted.

If Neandertals were replaced by immigrant amHs in Europe, as hypothesized by the RAO model, we would expect to find evidence of temporal overlap between Neandertals and amHs. This does, in fact, appear to be the case. The earliest modern human fossils in Europe date from around >30 Ka at Kent's Cavern, Vogelherd and Kelsterbach to perhaps as old as >43 Ka at Bacho Kiro, Bulgaria (Smith et al., 1999), while the latest Neandertals date to ~28 at Vindija (Smith et al., 1999) and ~27 Ka at Zafarraya (Hublin et al., 1995). The overlap of (at least) a few thousand years between the earliest AMHs and the latest Neandertals in Europe supports the idea that there was not enough time for the amHs to have evolved from Neandertals in Europe (Bräuer, 1989; but see Frayer, 1997; Stringer, 1984). Likewise, dates for Neandertal and early amHs sites in the Near East (Grün and Stringer, 1991; Schwarcz et al., 1988) indicating the probable coexistence of, or alternation between, these two groups would argue against an ancestral role for the Near East Neandertals in the origins of amHs. However, because MRE advocates view amHs and Neandertals as racial variants of the same species, they do not consider chronological overlap between these hominid groups as a problem. Rather, chronological overlap is held to bolster the view that the two were interbreeding. One example of possible interbreeding comes from Portugal. The Lagar Velho 1 child,

dating to ~24.5 Ka and buried with Upper Paleolithic tools, has been interpreted as a Neandertal-amHs hybrid because it presents a mosaic of Neandertal and modern human morphological characters (Duarte et al., 1999).

If, as some RAO supporters believe, Neandertals were members of a distinct species of the genus *Homo*, then they would be expected to exhibit a unique combination of shared features. This, alone, would not exclude them from contributing to later human evolution as these features could be primitive in nature. However, if they also exhibit a significant number of autapomorphies, the case for Neandertal ancestry is somewhat weakened. A number of researchers have identified what they consider unique Neandertal traits (Rak et al., 1994; Schwartz and Tattersall, 1996; Stringer, 1993b; Stringer et al., 1984; Tillier, 1989). Rak's work on Neandertal facial architecture reinforces the view that the 'classic' Neandertal face is unique, representing a "departure from the generalized fundamental architectural pattern that characterizes all the species of the genus *Homo*" (Rak, 1986: 163). That some autapomorphic characters (e.g., medial pterygoid tubercle) are found in Neandertal infants is interpreted as evidence supporting that these characters have a strong genetic component (i.e., they do not develop in adults solely in response to environmental stressors) (Rak et al., 1994; Tillier, 1989).

The claim that Neandertals exhibit a significant number of autapomorphic characters has been challenged (Franciscus, 1999; Trinkaus and Zilhão, 1999; Wolpoff et al., 1994). Purported Neandertal autapomorphies can be found in early modern European populations (e.g., horizontal-oval form of mandibular foramen: Frayer et al., [1993]) and others are absent in some Neandertals (e.g., posterior placement of the mental foramen:

Trinkaus [1993]). Furthermore, supporters of MRE have claimed that evidence exists for gradual evolution of modern morphology from the Neandertal condition in Central Europe (Frayer et al., 1993; Smith, 1982; Wolpoff et al., 2000; Wolpoff et al., 1981b). Most recently, Wolpoff et al. (2000) have argued that a dual ancestry for Mladeč males including both early modern humans represented by Skhul/Qafzeh and European Neandertals) cannot be ruled out based on their morphometric similarity to both groups. In addition, they report finding supposed Neandertal autapomorphies in the Mladeč males.

RAO advocates counter that Upper Paleolithic fossils show neither the most diagnostic Neandertal apomorphies nor "transitional" morphologies. They assert that the "Neandertal features" found in early Upper Paleolithic modern humans are properly interpreted as plesiomorphic (e.g., large brow ridges, jaws and teeth: Stringer et al., [1984]), and as such they tell us nothing about the relationship between Neandertals and amHs. However, according to Duarte et al. (1999), the recently discovered Lagar Velho 1 child from Portugal, which has been interpreted as a Neandertal-amHs hybrid, challenges this view. This child demonstrates a mosaic of characters – some of which are thought to be unique to Neandertals (e.g., its femorotibial length proportions and lower limb hypertrophy pattern) and others that are thought to be unique to amHs (e.g., chin development).

The problem of sorting out the biological relationship between Neandertals and amHs is confounded by a lack of agreement regarding how morphological characters should be interpreted. Much of the conflict can be attributed to disagreement over the

polarity (primitive vs. derived nature) of certain features, as well as the definition and identification of homologous features (see Gambier, 1997; Lahr, 1997; Smith and Harrold, 1997; Stringer, 1982). This may be due, at least in part, to the nature of working with certain skeletal features that are generally more plastic and affected more by the environment (diet, behavior, etc.) than are teeth.

Objectives

Unlike previous studies of Neandertal morphology, this research focuses on the dentition. The primary objective is to investigate how dental morphology can contribute to understanding evolutionary relationships among Middle to Late Pleistocene hominids. Specifically, my goal is to assess the relationship between Neandertal and amHs samples though phenetic and phylogenetic analyses of postcanine tooth crown characters.

I have chosen to focus on postcanine teeth because, relative to the anterior teeth, these have received far less attention as regards modern human origins and the Neandertal problem. There seems to be an underlying assumption that the primary differences between Neandertal and amHs teeth lie in anterior tooth size (e.g., Brace, 1964) and/or morphology (e.g., Crummett, 1995), and that Neandertal molars and premolars are much like our own (Smith, 1976). One of the research goals is to test that assumption and use this information to test predictions generated by competing models of human origins.

Hypotheses to be addressed

To attain my primary objective, it is necessary to define the Neandertal dental pattern through a combination of primitive, derived and/or autapomorphic characters, and

to identify the parameters of Neandertal dental variability through time and across geographic space.

I acknowledge that in light of recent genetic research (e.g. Relethford, 1999), intermediate models – which combine aspects of both replacement and continuity (through admixture between amHs and archaic populations, and/or local evolution) – may be the most appropriate for understanding Late Pleistocene human evolution. However, these models are difficult to test from the fossil record, namely because it lacks the resolution needed to distinguish brief periods of hybridization from a more gradual evolution/assimilation process. Therefore, the following predictions derive from a more "strict" interpretation of MRE – one that predicts a "pattern of regional variation [that is] maintained throughout most of the Pleistocene" (Wolpoff et al., 1984: 463).

Dental Patterns: If Neandertals contributed significantly to the ancestry of amHs (either through direct evolution or mixed ancestry), they would be expected to lack significant numbers of dental autapomorphies.

Cladistic affinity: If Neandertals contributed significantly to the ancestry of amHs these groups would be expected to emerge as sister groups in a cladistic analysis, indicating descent from a recent common ancestor unique to them.

Phenetic affinity: If amHs evolved as the result of gradual *in situ* evolution (or extensive admixture with local archaic populations) Neandertals should be dentally more similar to early amHs from the same geographic region than they are to amHs from other geographic regions.

Significance

This project uniquely brings together temporal and geographic axes of variation in a phenetic and phylogenetic analysis of the issue of modern human origins. Excepting Crummett's (1995) study of shovel shaped incisors, neither geographic nor temporal variation in later Pleistocene hominid dental morphology has been the focus of anthropological study. This research will provide an independent evaluation of current biological and archaeological hypotheses concerning Neandertal affinities and modern human origins. Ultimately, this information may be useful to other researchers as a guide for assessing the affinities of specimens of uncertain taxonomic affiliation.

DENTAL ANTHROPOLOGY AND THE ORIGIN OF MODERN HUMANS

Introduction

Scott and Turner (1988:100) have pointed out that "a biological trait can be useful in historical-evolutionary analyses only if a significant component of its variation is genetic". Although interest in dental morphological variation and its distribution among populations was well-established early in the 20th century (Gregory, 1916; Hellman, 1928; Hrdlička, 1911; 1920; 1921), investigations into the genetic nature of dental traits did not begin until mid-century (Grüneberg, 1952; Kraus, 1951; Kraus and Furr, 1953; Lasker, 1950). Since then much effort has been expended to uncover the genetic basis of nonmetric dental traits (Bailey et al., 1997; Berry, 1976; Brothwell, 1963; Carbonell, 1963; Corruccini et al., 1986; Dahlberg, 1971; Goose and Lee, 1971; Harris and Bailit, 1980; Nichol, 1989; Scott, 1972; 1974; Sofaer, 1969; 1975; Sofaer and MacLean, 1970). More recently, study of Hox and homeobox genes has led to a finer level understanding of the genes that are involved in specifying certain aspects of the dentition, such as tooth differentiation (Weiss, 1990; 1994; 1998). Thus, population genetics, pedigree studies and, now, molecular studies all strongly support that dental morphology has a high genetic component.

Aside from their strong genetic component, there are several other reasons why dental nonmetric traits were chosen as the focus of this study. While the exact genetic basis for dental traits has not been fully demonstrated, tooth crown and root morphology provide a useful means to identify biological relationships among archaeologically derived human samples (Bailey et al., 1998; Dahlberg, 1951; 1963; 1965; Haeussler, 1985; 1996; Haeussler and Turner, 1992; Hanihara, 1977; Hanihara et al., 1975;

Hanihara, 1989; Harris and Bailit, 1980; Hawkey, 1998; Irish, 1993; 1997; Irish and Turner, 1990; Lipschultz, 1997; Lukacs, 1983; 1986; Lukacs and Walimbe, 1984; Scott et al., 1988; Sofaer et al., 1986; Turner, 1969; 1983; 1987; 1990b; 1993; 1995; Zubov, 1973). The human dentition is evolutionarily conservative and changes little over many generations (Scott and Turner, 1988). Teeth also preserve very well and are often the only undamaged remains recovered in an archaeological context. Finally, owing to their morphological complexity, teeth contain a large array of metric and non-metric information. For example, Morris (1965) identified 200 morphological crown traits and speculated there might be even more.

Although of interest to anthropologists for decades, it took many years for dental morphological standards – the Arizona State University Dental Anthropology System (ASUDAS) – to be developed and made available on a wide scale basis for comparative studies (Turner et al., 1991). The system, which grew out of the work of A.A. Dahlberg (1956), is becoming the worldwide standard for morphological study. It has served as the basis for numerous studies aimed at deciphering population relationships among contemporary humans (e.g., Bailey et al., 1998; Haeussler, 1996; Hanihara, 1989; 1992; Hawkey, 1998; Irish, 1993; Lipschultz, 1997; Nichol, 1990; Turner, 1990a; 1990b). The ASUDAS currently consists of more than 36 crown and root traits, which are scored using a combination of visual representations and written descriptions (Turner et al., 1991). The traits that are included in the ASUDAS are relatively easy to score, can be scored even after moderate wear, and have proven useful in characterizing intra- and inter-population variability and relationships. It is only recently that attempts have been

made to use this system (or some version of it) to address biological relationships among Upper Pleistocene fossil hominids (Bailey, 2000b; Bailey and Turner, 1999; Coppa et al., 2001; Crummett, 1994; Irish, 1998; Stringer et al., 1997).

Neandertal dental morphology (Taurodont molars and beyond)

Neandertal teeth are often perceived as being much like our own. This perception has a long history. Boule and Vallois (1957) felt that the general characters of all human teeth were very ancient, stating that of Neandertals "(N)o important characteristic distinguishes the incisors, the canines or the premolars from the corresponding teeth in modern man." What differences they did observe between Neandertals and amHs (e.g., lack of upper molar hypocone reduction and presence of five cusped lower molars) were thought to be of primitive nature having no phylogenetic value.

During excavations of Krapina Cave, Gorjanovič -Kramberger (1904; 1906) recognized several unusual dental characters in the Neandertal fossils he uncovered. These included the incisor peculiarities of shoveling, large lingual tubercles and also taurodont, or "bull-toothed", molar roots. Keith (1913; 1924) asserted that taurodont roots were a unique Neandertal trait stating that

> Although taurodontism of a high degree is not present in every individual of the Neanderthal type, it is only in members of this race that high degrees of it have been observed (Keith, 1924, p. 253).

This assertion has largely held up to scrutiny in the fossil record (Patte, 1959; Skinner and Sperber, 1982; Trinkaus, 1983). Those who have quantified the character (e.g., Pindborg, 1970) have found the frequency of taurodont molars to be very low in contemporary modern humans (less than 0.1%). It is typical for descriptions of

Neandertal morphology to identify variably present taurodontism as one of the traits that distinguishes them from other hominids (e.g., Day, 1977; Hillson, 1986; Klein, 1999; Stringer and Gamble, 1993).

In addition to taurodont molars, Neandertals are notable for their shovel-shaped maxillary incisors. In mild expression, shoveling (the presence of lingual marginal ridges) is considered the normal hominoid condition (Hillson, 1986). These features are effectively ubiquitous in early *Homo* and Australopithecines (Kimbel et al., 1997; Robinson, 1956; Tobias, 1991; Wood, 1991). However, in Neandertals the expression of this character is especially marked. Gorjanovič -Kramberger (1906) was one of the first to document shovel shaped incisors in the fossil record, having recognized its strong expression to be one of the most unique aspects of the Krapina teeth.

Hrdlička (1911; 1920; 1921) was the first to quantify the variation of shovel-shaped incisors in recent humans and to describe its evolutionary and racial significance. Recently, Mizoguchi (1985) and Crummett (1994; 1995) have attempted to define shovel-shaping in terms of the whole tooth rather than the marginal ridges exclusively. Mizoguchi (1985) included expression of lingual tubercles in his definition(s), while Crummett (1994) proposed that shovel shaping is best expressed in three dimensions: marginal ridge development, lingual tubercles and labial crown convexity. In Neandertals, marginal ridge development is ubiquitous and often quite marked in its expression. Lingual tubercles are also common, and take the form of well-developed single or multiple ridges on the central incisor and, often, cusp-like tubercles in the lateral incisor. Labial convexity, which also occurs in high frequency in Neandertals (Bailey,

2000a; Crummett, 1994; Tillier, 1979; 1991), is sometimes so marked it exceeds the highest grade on the ASUDAS scale (Bailey, 2000a). In sum, Neandertal anterior teeth have been characterized by a combination of incisor shoveling, lingual tubercles and labial convexity (Bailey, 2000a; Crummett, 1995; Patte, 1959; Smith, 1989). Although all three characters can be found in mild to moderate degrees in other hominids, their combination and, especially, their marked expression appears to be unique to this group (Bailey, 2000a; Crummett, 1995).

Few other dental traits have received as much attention as taurodont roots and shovel-shaped incisors. During the middle part of the last century descriptive studies of Neandertal teeth alluded to additional unique dental characters in Neandertals (e.g. Genet-Varcin, 1966; Patte, 1959). More recently, Zubov (1992a; 1992b) noted that the epicristid, or mid-trigonid crest, of the lower molars occurred in high frequency in Neandertals. However, little has been done to systematically pursue these suggestions. Instead, monographic studies of particular fossils have dominated the literature (Bordes and Lafille, 1962; de Lumley, 1972; Fraipont, 1936; Fraipont and Lohest, 1887; Piveteau, 1959; Piveteau et al., 1963; Tillier, 1983).

Perhaps it was because the implicit goals of early studies of Neandertal morphology were to report new information and to ascertain their phylogenetic position vis-à-vis apes and modern humans (i.e., are they more ape like or more human like?) that little attention was paid to some of the more minor variants of Neandertal dental morphology. As a result, the general impression today is similar to that espoused by Boule and Vallois (1957) nearly half a century ago. That is, except for a few characters,

Neandertal teeth are much like our own. This, however, remains to be determined. Recent research based on traits observed in contemporary modern humans indicates that Neandertals exhibit a unique dental pattern relative to all living human groups (Bailey, 2000a; 2000b; Stringer et al., 1997; Tyrell and Chamberlain, 1998). However, the study of additional traits that are *not* present in contemporary modern humans are necessary to fully understand this pattern and its phylogenetic significance (Bailey, 2001; 2002).

Dental morphology and theories of modern human origins

Traditionally, dental metrics have received more attention than dental morphology in studies focusing on modern human evolution and relationships among Middle to Late Pleistocene hominids (e.g., Brace, 1967; Bytnar et al., 1994; Calgano and Gibson, 1991; Frayer, 1977; Macchiarell and Bondioli, 1986; Sheets and Gavan, 1977; Wolpoff, 1971). However, in the beginning of the last century certain dental morphological traits, particularly incisor morphology, played an integral role in hypotheses about the origins of modern humans. Just as it does today, this role involved drawing inferences about continuity, or lack there of, between fossil and recent groups.

For example, Weidenreich (1937) held that the presence of large projecting tubercles established a close link between fossil hominids and amHs. Moreover, he asserted that shovel shaped incisors were evidence of continuity between Asian *Homo erectus* and modern Chinese. This latter sentiment has been echoed in more recent publications (Crummett, 1994; Frayer et al., 1993). Frayer et al. (1993) argued that:

> Perhaps the most inarguable indication of morphological continuity is the high frequency in living Asians of the strong manifestations of maxillary incisor shoveling, which also characterizes virtually every fossil Asian hominid preserving these teeth. (p. 25)

However, the dental *pattern* observed in modern Northeast Asians (Sinodonty: Turner, 1983) is actually characterized by maxillary incisors with strong marginal ridges both lingually (shovel-shaped) *and* labially (double shoveling). *Homo erectus* incisors may have strong lingual shoveling but they lack double shoveling, which tends to give the tooth a labially concave shape. Instead, Asian *Homo erectus* incisors have moderately labially *convex* incisors. Moreover, the dental *pattern* observed in modern Northeast Asians most likely has a relatively recent origin, dating to only about 15,000 years ago (Turner, 1992b).

Based primarily on a limited literature review and his personal observations, Zubov (1992b) claimed that certain dental morphological features (shovel-shaped incisors à la Mizoguchi [1985] and the epicristid or mid-trigonid crest) support Bräuer's (1984) Afro-European *sapiens* hypothesis (replacement with hybridization). He maintained that modern incisor morphology, in particular, has deep African roots. However, his assertion that

> [T]he processes of hybridization within the genus *Homo* on all levels and stages supports the hypothesis of a reticular pattern as the characteristic mode of human evolution since at least the time of *Homo erectus.* (p. 7)

is probably a better description of MRE (in its most recent form) than any replacement model.

Focusing on phylogenetic rather than phenetic relationships Smith (1989) came to different conclusions regarding continuity between Neandertals and amHs in the Near East. Her examination of deciduous dental morphology and comparisons to earlier

hominids suggested to her that the unique incisor morphology and taurodontism seen in Neandertals are autapomorphic rather than plesiomorphic traits. Based on this assessment of trait polarity, and also on distinctive deciduous upper first molar cusp form in Neandertals, she concluded that there was no evidence to support the hypothesis of continuity between Neandertals and amHs in the Near East.

All told, until recently hypotheses about modern human origins based on dental morphology have been based on one or few characters rather then the entire "dental morphological package." Systematic studies of a large number of dental morphological traits have only recently been brought to bear on the issue of modern human origins (Bailey, 2000b; Bailey and Turner, 1999; Crummett, 1994; Irish, 1998; Stringer et al., 1997; Tyrell and Chamberlain, 1998), probably owing to the fact that until recently (Turner et al., 1991) methods for collecting morphological data had not been formally outlined.

Using the (slightly modified) Arizona State University dental anthropology system (ASUDAS), Crummett (1994) investigated Old World regional patterns of incisor variation in fossil hominids and contemporary modern humans. She hypothesized that regional patterns of morphological variation would be maintained over time if modern humans had evolved through the process of multiregional evolution. Her dental data from Northwest Europe did not appear to support this hypothesis, and patterns in other regions were more ambiguous, leading her to conclude that incisor morphology could not refute either of the two competing hypotheses for modern human origins.

In contrast to Crummett's study, which focused on a single dental field (incisors) and a few morphological traits, Stringer et al. (1997), Irish (1998) and Tyrell and Chamberlain (1998) utilized a larger suite of dental morphological traits (based on the ASUDAS) to investigate relationships among contemporary humans and to assess Africa's role in modern human origins. Each of these studies reached similar conclusions.

Stringer et al. (1997) applied a cladistic analysis to contemporary human groups using the Krapina Neandertal sample as an outgroup to root the modern human tree. Overall their results appear to support the RAO model. The African sample, in each case, was the first population to diverge, which they interpreted as indicating greater similarity to Krapina Neandertals. They attributed this similarity to retained primitive dental characters in the African sample. They also found that sub-Saharan Africans were most similar to a hypothetical (dental) common ancestor for amHs. They also suggested that MRE predicts a closer relationship between European (Krapina) Neandertals and contemporary Europeans than other contemporary human groups; a prediction not held up by their analysis.

Irish (1998) used Mean Measure of Divergence analysis of C.A.B. Smith (in Berry and Berry, 1967) to assess phenetic similarity among contemporary humans, Plio-Pleistocene hominids and Krapina Neandertals. His results indicated that Sub-Saharan Africans 1) were dentally dissimilar to other modern humans groups, 2) showed greater heterogeneity than other modern groups, and 3) retained the most primitive dental traits

(i.e., those that are also present in Plio-Pleistocene hominids). Irish (1998) felt that these findings provided additional support for the RAO model.

Tyrell and Chamberlain (1998) transformed Stringer et al.'s (1997) data into genetic diversity coefficients to investigate genetic distances among contemporary humans and Krapina Neandertals. They found that the average genetic distance between the Krapina Neandertals and contemporary humans (1.73) was much greater than the mean pair-wise distance within contemporary humans (1.01). Like Stringer et al. (1998), they found that the Krapina Neandertals did not closely resemble modern Europeans, as may be predicted by MRE (but see Relethford, 2001a for an argument against the validity of this prediction).

Two recent studies used the ASUDAS to examine the dental relationship between Neandertals and amHs more closely. Bailey and Turner (1999) compared dental morphological variation in three regionally defined Neandertal samples to that of early amHs and contemporary Europeans. The results from mean measure of divergence analysis (MMD) indicated that, dentally, Neandertals were more similar to each other than they were to either modern human sample. The analysis also indicated there was no sign of regional continuity between Neandertals and amHs from the same region (in this case, Europe and the Near East).

Bailey (2000b) compared dental trait frequencies of Late Pleistocene hominids (Neandertals, early and Upper Paleolithic amHs) with those of several contemporary modern human populations. Results from the 18-trait MMD analysis were used to produce a dendrogram on which Neandertals and modern humans formed two distinct

clusters (Fig. 2.1). Within the modern human cluster two sub-clusters were apparent: one linked Upper Paleolithic Europeans with contemporary North Africans and Europeans; the other linked the early amHs (Qafzeh/Skhul) sample with contemporary Sub-Saharan Africans and Late Pleistocene Africans. These results failed to support the hypothesis that Upper Paleolithic Europeans are phenetically more similar to Neandertals than Neandertals are to other geographical groups of contemporary modern humans, as might be predicted by MRE (but again, see Relethford, 2001a). In addition, the fact that the earliest amHs (Qafzeh/Skhul) dentitions are phenetically more like living Africans than like Near East Neandertals tentatively suggests that if genes were flowing between Neandertals and amHs in the Near East, it did not significantly impact dental morphology.

These results indicate that a unique Neandertal dental morphological pattern is beginning to emerge. This pattern appears to go beyond taurodontism and anterior tooth size and combine plesiomorphic and apomorphic traits (Bailey, 2002). The primary question here is what this unique pattern means in terms of the evolutionary relationship between Neandertals and amHs.

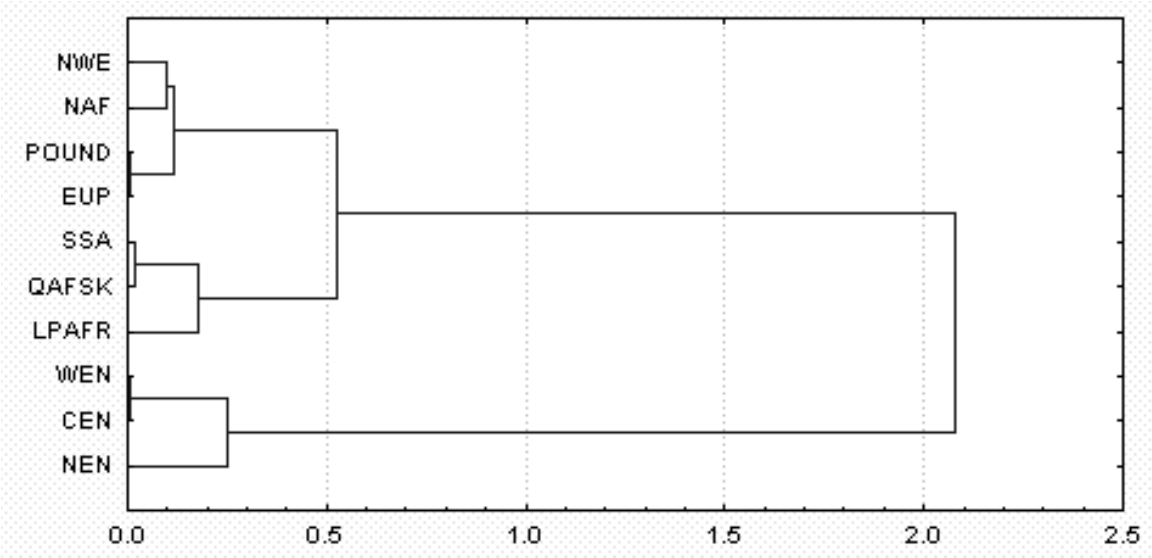


Fig. 2.1. Dendrogram of the results of an 18-trait MMD analysis: Ward's method.

(NWE: North West Europe; NAF: North Africa; POUND: Poundbury, England; EUP: European Upper Paleolithic; SSA: Sub-Saharan Africa; QAFSK: early amHs from Qafzeh and Skhul; LPAFR: Late Pleistocene Africa; WEN: West European Neandertal; CEN: Central European Neandertals; NEN: Near East Neandertal)

MATERIALS

Data were collected on postcanine teeth of fossil and contemporary humans. The modern human data were collected on museum skeletal collections from the American Museum of Natural History, New York and the Natural History Museum, London. Tooth wear, pathology, antemortem and postmortem tooth loss made finding adequate samples difficult and time consuming. A large number of individuals had to be examined just to find the sample sets used in these analyses.

The fossil human data were collected from a variety of foreign institutions. I examined nearly every Neandertal and Upper Paleolithic specimen with adequately preserved teeth for which permission for study was granted. The fossils include Middle Pleistocene archaic *Homo sapiens*, Neandertals, late Pleistocene early amHs, Upper Paleolithic amHs and contemporary amHs. Details of the sample compositions are given below.

Anatomically modern *Homo sapiens* (amHs) sample

The amHs samples were divided into three temporal groups: Early amHs, Upper Paleolithic amHs and contemporary amHs. Table 3.1 lists the site, the number of individuals, the scoring method (cast vs. original), the age and the appropriate bibliographic reference for each of the Early and Upper Paleolithic amHs samples. Table 3.2 lists the population, number of individuals, group assignment and geographic origin for the contemporary amHs sample. Data collected on all contemporary amHs were obtained directly from original skeletal material. To maximize the amount of information that could be gathered at each institution dentitions had only to preserve at least one tooth

representing each tooth group (premolars, molars) on either the left or right side to be included in the sample. Data on the fossil amHs samples were collected from both original fossils and also high resolution casts where studying the original fossils was not possible or where adequate photographs of the originals were not obtained. Requirements for including the fossil samples were more lenient than for the contemporary amHs samples, and any tooth with some visible morphology was scored and used in the analysis.

Neandertal sample

The Neandertal sample comprises individuals from both Europe and Western Asia. I based my justification for including particular fossils in the Neandertal sample on a review of the relevant literature. Taxonomic assignment is most often based on skeletal or skull morphology, but sometimes is it based on its archaeological context and/or age. Occasionally, tooth morphology (e.g., taurodont molars) has been used in assigning a fossil to a particular group, but it is very rarely the sole basis for its taxonomic assignment. To address the question of change over time, the sample was divided into early and late temporal sets based on oxygen-isotope (OI) stages (early = oxygen isotope stage 5+ and late = oxygen isotope stages 2 to 4). Table 3.3 lists the fossils/sites, number of individuals, geographic origin, scoring method, Group/OI stage, as well as references to the source(s) of the age and taxonomic assignment.

Archaic *Homo sapiens* sample

The archaic *Homo sapiens* sample consists of European Middle Pleistocene hominids that have been variously referred to as ante-Neandertals, pre-Neandertals, and

Homo heidelbergensis. Typically, these fossils exhibit a combination of primitive or *Homo erectus*-like characters (e.g., large brow ridges, receding chin) and more "advanced" characters (more modern nasal and temporal bone morphology, increase in brain size) (Rightmire, 2001). In addition, they lack the suite of diagnostic characters of either amHs or Neandertals. All data were collected on original specimens. Table 3.4 provides a list of the fossils as well as references to sources of the age and taxonomic determination.

Homo erectus sample

The *Homo erectus* samples serves as an outgroup for the cladistic portion of the analysis. It consists of fossils from Java, Asia, North Africa and East Africa. With the exception of the North African fossils, all data were collected from high-resolution casts. Table 3.4 gives the sites, number of individuals, age and geographic origin of the specimens, as well as references to sources of the age and taxonomic determination.

TABLE 3.1. Details of the fossil modern human sample, with references for age and taxonomic designation/description.

Group/Site	No[1]	Origin	Age[2]/Context	Reference[3]	Method
Early amHs					
Qafzeh	7	Israel	90-120	1,2,3	originals & casts
Skhul	2	Israel	81-101	1,4	originals & casts
Upper Paleolithic amHs					
La Madeleine	1	France	Magdalenian	5,6	original
St. Germaine-la-Rivière	2	France	Magdalenian	7,8	originals
Le Vachons	1	France	Perigordian	9,10	original
Grotte des Abeilles	2†	France	Magdalenian	11	originals
La Ferrassie	3	France	Aurignacian	12	originals
La Gravette	1	France	Gravettian	13	original
Isturitz	6	France	Mixed U.P.: Aurignacian Gravettian, Magdalenian	14,15,16	originals & casts
Fontéchevade	2	France	Aurignacian or Perigordian	17,18	casts
Grotte de Rois	2/12†	France	Aurignacian	16,19,20,21	originals & casts
Abri Labattut	1	France	Solutrean	22,23	original
Gough's Cave	3	England	Magdalenian	24	original
Oberkassel	1	Germany	Magdalenian	25,26	original
Brno	1	Czech Rep	Gravettian	29, 30	original
Dolní Věstonice	7	Czech Rep	Gravettian	31, 32,33, 34	original
Pavlov	3	Czech Rep	Gravettian	35, 33	original
Miesslingtal	1	Austria	Aurignacian	27, 28	original
Mladeč	2/3†	Austria	Aurignacian	36, 37	original

TABLE 3.1. (notes)

[1] † number of isolated teeth. Unless indicated by †, "No." indicates number of individuals scored. However, some individuals may be represented by a single tooth.

[2]Aurignacian = 40-25 kya; Gravettian = 27-21 kya; Solutrean = 22-19 kya; Magdalenian = 18-12kya (ages are approximate)

[3] 1, Vandermeersch, 1991; 2, Grün and Stringer, 1991; 3, Schwarcz et al, 1988; 4, Stringer et al, 1989; 5, Peyrony, 1927; 6, de Sonneville-Bordes, 1959; 7, Vaufrey, 1935; 8, de Sonneville-Bordes, 1956; 9, Ferembach, 1956; 10, Bouyssonie and de Sonneville-Bordes, 1956; 11, Gambier and Houet, 1993; 12, Delibas, 1984; 13, Lacorre, 1960; 14, Zilhao and d'Errico, 1999; 15, Gambier, 1997; 16, St. Perier and St. Perier, 1952; 17, Vallois, 1958; 18, Henri Martin, 1957; 19, Mouton and Joffroy, 1958; 20, Oakley, 1971; 21, Mouton, 1958; 22, Breuil and Lantier, 1951; 23, Smith, 1966; 24, Smith, 1992; 25, Bonnet, 1919; 26, Bonnet, 1913-1914; 27, Felgenhauer, 1950; 28, Szombathy, 1950; 29, Jelínek, 1959; 30, Jelínek, 1991; 31, Klíma, 1988; 32, Svoboda and Vlček, 1991; 33, Klíma and Kukla, 1963; 34, Vogel and Zagwijn, 1967; 35, Vlček, 1961; 36, Szombathy, 1900; 37, Szombathy, 1925

TABLE 3.2. Contemporary amHs sample

Population	Geographic origin
Nubian	N. Africa (NAF, n=31)
Ashanti Abome Dahomey Nigeria Kamerun Mandingo	West Africa (WAF, n=19)
British Neolithic Hungary Bosnia Austria Yugoslavia Bulgaria Greece Crete	Europe (EUR, n=54)
Japan China Korea	Northeast Asia (NEA, n=21)
Tel Hesi Jericho	Near East (WAS, n=18)
India	India (IND, n=20)
Australia New Guinea	Australasia (AUST, n=49)

TABLE 3.3. Details of the Neandertal sample with references for age and taxonomic designation/description.

Fossil	No[1]	Origin	OI Stage[2]	Context	Justification	Reference[3]	Method
Breuil	2	Italy	OI3	Mousterian	cranial morphology	1	original
Fenera	2	Italy	uncertain	Mousterian	cranial morphology(2); dental metrics/ morphology (4)	2	original
Guattari	2	Italy	OI 4 (2); OI 5 (3)	Mousterian	mandibular morphology (2); cranial morphology(3)	3,4(2),5,6(3),7,8	original
Melpignano	1	Italy	OI 5	none	tooth size/root morphology	9	original
Taddeo	3	Italy	uncertain	Mousterian	tooth size/morphology	10	original
Le Fate	4	Italy	OI 5	Mousterian	cranial and mandibular morphology	11,12	original
Gibraltar	1	Spain	OI 3	Mousterian	cranial characters	13,14,15	cast
Hortus	5	France	OI 3	Mousterian	mandibular morphology	16,17	casts/ original
Arcy-sur-Cure	2	France	OI 3	Chatelperonian	cranial morphology	18,19,20	casts
Combe-Grenal	1	France	OI 3	Mousterian	mandibular morphology	21,22,23	original
La Quina	2	France	OI 4	Mousterian	mandibular morphology cranial characters (18) taurodontism	24,25,26,27,28	original
Le Moustier	1	France	OI 3	Mousterian	skeletal morphology	29,30,31	original
Monsempron	2	France	OI 5	Mousterian	mandibular morphology	32,33	casts
Petit Puymoyen	4	France	OI 4	Mousterian	mandibular morphology	34,35	casts
Regourdou	1	France	OI 4	Mousterian	mandibular morphology; taurodontism	36,37,38	original
Roc de Marsal	1	France	OI 3	Mousterian	cranial morphology	39,40	original

TABLE 3.3. (continued)

Fossil	No[1]	Origin	OI Stage[2]	Context	Justification	Reference[3]	Method
Pontnewydd	1/ 11†	Wales	OI 7	Acheulean	cranial morphology	41,42	casts
Vindija	5	Croatia	OI 3	Mousterian	cranial morphology	43,44	original
Kůlna	1	Czech Republic	OI 3	Mousterian	cranial morphology	45,46,47,48	original
Ochoz	1	Czech Republic	OI 3	Mousterian	cranial/mandibular characters	49, 50, 51	original
Kebara	1	Israel	OI 4	Mousterian	cranial/postcranial morphology	52,53	cast/ original
Amud	1	Israel	OI 4	Mousterian	cranial/postcranial morphology	54,55	cast/ original
Krapina	32/ 25†	Croatia	OI 6	Mousterian	cranial characters; taurodontism	56,57,58,59	original
Ehringsdorf	3	Germany	OI 5(61) OI 7(62)	Mousterian	cranial morphology	60,61,62,63	original
Taubach	1	Germany	OI 5	Middle Paleolithic	Archaeological context	64,65	original
Spy	2	Belgium	OI 5	Mousterian	Cranial/skeletal morphology	66,67	original
Saccopastore	2	Italy	OI 5	Mousterian	cranial morphology	68,69	original
Tabun	3	Israel	OI 5	Mousterian	skeletal morphology; mandibular morphology	70,71,72	original
Shanidar	1	Iraq	OI 4	Mousterian	cranial/postcranial morphology	73,74	cast/ original

TABLE 3.3. (notes)

[1] † number of isolated teeth. Unless indicated by †, "No." indicates number of individuals scored. However, some individuals may be represented by a single tooth.

[2] OI Stage 3: 24-59 kya; OI Stage 4: 59-71 kya; OI Stage 5: 71-128 kya; OI Stage 6: 128-186 kya; OI Stage 7: 186-245 kya.
Late Neandertal = OI Stage 3&4; Early Neandertal = OI Stage 5-7

[3] 1, Manzi and Passarello, 1995; 2, Villa and Giacobini, 1996; 3, Blanc, 1939; 4, Sergi, 1954; 5, Blanc, 1951; 6, Sergi and Ascenzi, 1955; 7, Grün and Stringer, 1991; 8, Schwarcz et al, 1991; 9, Bologna et al, 1994; 10, Vigliardi, 1968; 11, Giacobini and de Lumley, 1984; 12, Giacobini et al, 1984; 13, Garrod et al, 1928; 14, Tillier, 1982; 15, Vogel and Waterbolk, 1964; 16, Piveteau, 1963; 17, de Lumley, 1982; 18, Leroi-Gourhan, 1958; 19, Leroi-Gourhan, 1961; 20, Hedges et al, 1994; 21, Bordes, 1955; 22, Piveteau, 1957; 23, Bowman and Sieveking, 1983; 24, Henri-Martin, 1911; 25, Henri-Martin, 1923; 26, Henri-Martin, 1926; 27, Henri-Martin, 1964; 28, Mellars, 1996; 29, Klaatsch and Hauser, 1909; 30, Mellars and Grün, 1991; 31, Valladas et al, 1986; 32, Vallois, 1952; 33, Oakley, 1971; 34, Favraud, 1908; 35, Vandermeersch, 1965; 36, Piveteau, 1959; 37, Piveteau, 1963-1965; 38, Bonifay, 1964; 39, Bordes and Lafille, 1962; 40, Madre-Dupouy, 1992; 41, Green, 1981; 42, Green 1984; 43, Wolpoff, et al, 1981; 44, Smith et al, 1999; 45, Jelínek, 1966; 46, Jelínek, 1989; 47, Rink et al, 1996; 48, Valoch, 1968; 49, Jelínek, 1962; 50, Rzehak, 1905; 51, Vañura, 1965; 52, Tillier, 1995; 53, Bar-Yosef et al, 1988; 54, Suzuki and Takai, 1970; 55, Rink et al, 2001; 56, Radovčić et al, 1988; 57, Smith, 1976; 58, Wolpoff, 1979; 59, Rink et al, 1995; 60, Smith, 1984; 61, Steiner, 1979; 62, Grün, 1988; 63, McBurney, 1950; 64, Schmidt, 1912; 65, Eeiman-Zeuner, 1940; 66, Fraipont and Lohest, 1887; 67, Zeuner, 1940; 68, Sergi, 1958; 69, Serge, 1948; 70, Stefan and Trinkaus, 1998; 71, Mercier et al, 1995; 72, Schwarcz et al, 1998; 73, Trinkaus, 1983; 74, Solecki, 1963.

TABLE 3.4. Details of the archaic Homo sapiens *and* Homo erectus *samples, with references for age and taxonomic designation/description*

Site	No.[1]	Origin	Age	Reference[2]	Method
Archaic *Homo sapiens*					
Arago	3/12†	France	~450 Ka	1,2,3	original/casts
Montmaurin	1	France	~200 Ka	4,5,6	cast
Mauer	1	Germany	~400-500 Ka	7,8	original
Steinheim	1	Germany	~225 Ka	9,6	original
Petralona	1	Greece	150(11)-250(12) Ka	10,11,12	original
Fontana Ranuccio	3†	Italy	~400 Ka	13	original
Homo erectus					
Sidi Abderrahman	1	North Africa	~600 Ka	14,15	original
Ternifine/Tighenif	2/2†	North Africa	~ 500-700 Ka	15,16,17	original
Thomas	1	North Africa	~600 Ka	18	original
Koobi Fora					
(806, 820, 992)	3	East Africa	1.6-1.4 Ma	19,20	casts
(1506,1812)	2	East Africa	~1.9 Ma	19	casts
(807, 3733)	2	East Africa	1.4-1.8 Ma	19,21	casts
West Turkana WT15000	1	East Africa	~1.6 Ma	22	casts
Olduvai				23	casts
OH15	1	East Africa	~1.6Ma		
OH22	1	East Africa	~500 Ka	24	casts
Zhoukoudian	13†	China	250-600 Ka	25,26,27	casts

TABLE 3.4. (notes)

[1] † number of isolated teeth. Unless indicated by †, "No." indicates number of individuals scored. However, some individuals may be represented by a single tooth.

[2] 1, de Lumley and de Lumley, 1971; 2, Iacumin, 1996; 3, Yokoyama and Nguyen, 1981; 4, Billy and Vallois, 1977; 5, Vallois, 1956; 6, Schwartz and Tattersall, 2002; 7, Schoetensack, 1908; 8, Cook et al, 1982; 9, Morant, 1938; 10, Stringer, 1983; 11, Grün, 1996; 12, Hennig et al, 1981; 13, Serge and Ascenzi, 1984; 14, Arambourg and Biberson, 1954; 15, Arambourg and Biberson, 1955; 16, Arambourg and Hoffstetter, 1963a; 17, Arambourg and Hoffstetter, 1963b; 18, Sausse, 1975; 19, Feibel et al, 1989; 20, Wood, 1991; 21, Curtis et al, 1975; 22, Walker and Leakey, 1993; 23, Leakey, 1965; 24, Rightmire, 1990; 25, Weidenreich, 1943; 26, Grün et al, 1997; 27, Wu et al, 1985

METHODS

Terminology

The dental terminology presented here is derived from a number of sources, including Kraus et al. (1969), Carlsen (1987), Scott and Turner (1997) and Suwa (1990). Figure 4.1 provides the basic terminology used for features on both the tooth crown and root surfaces. Table 4.1 gives the terms used for the premolar and molar tooth crowns, and for some specific morphological characters referred to in the text. Figures 4.2 through 4.5 illustrate these features. Table 4.2 gives the abbreviations, together with their key tooth type, for the dental traits used in this analysis.

TABLE 4.1. Terms used in text. Numbers refer to Figs. 4.2-4.5.

Ref. #	Feature	Ref #	Feature
1	Protocone (Cusp 1)	17	Distal marginal ridge
2	Paracone (Cusp 2)	18	Transverse crest
3	Metacone (Cusp 3)	19	Mesial accessory ridge
4	Hypocone (Cusp 4)	20	Distal accessory ridge
5	Protoconid (Cusp 1)	21	Essential crest (buccal and lingual)
6	Metaconid (Cusp 2)	22	Accessory marginal tubercle
7	Hypoconid (Cusp 3)	23	Mesial marginal accessory tubercles
8	Entoconid (Cusp 4)	24	Lower Molar Cusp 6 (entoconuild)
9	Hypoconulid (Cusp 5)	25	Upper Molar Cusp 5 (hypoconule)
10	Groove pattern (Y)	26	Lower Molar Cusp 7 (metaconulid)
11	Accessory Lingual cusps (P_{34})	27	MaxPAR
12	Anterior fovea (mesial fossa)	28	Carabelli's Cusp
13	Posterior fovea (distal fossa)	29	Deflecting wrinkle
14	Lingual groove	30	Mid-trigonid crest
15	Sagittal sulcus (central groove)	31	Distal-trigonid crest
16	Mesial marginal ridge		

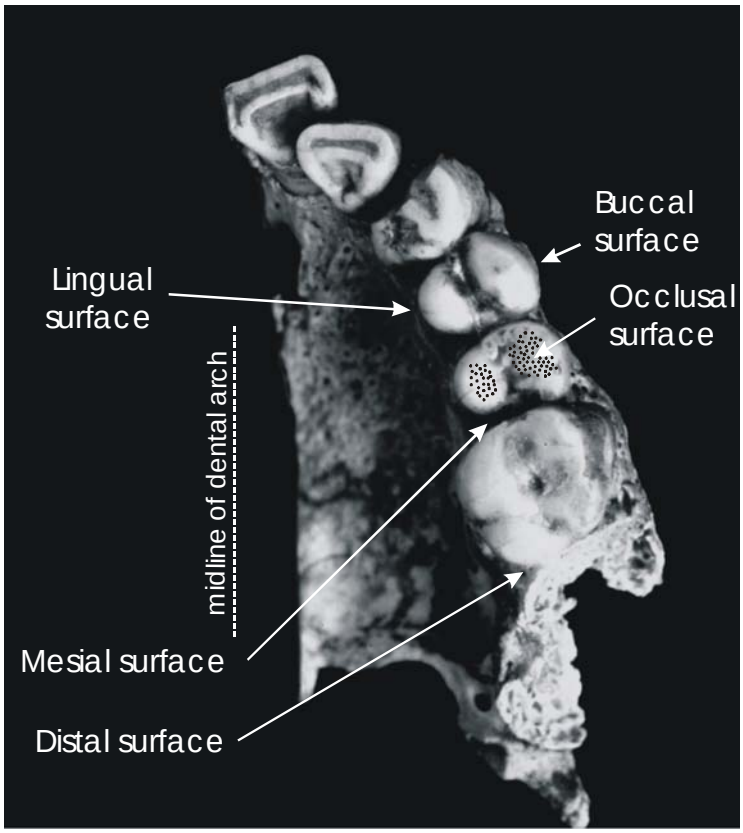
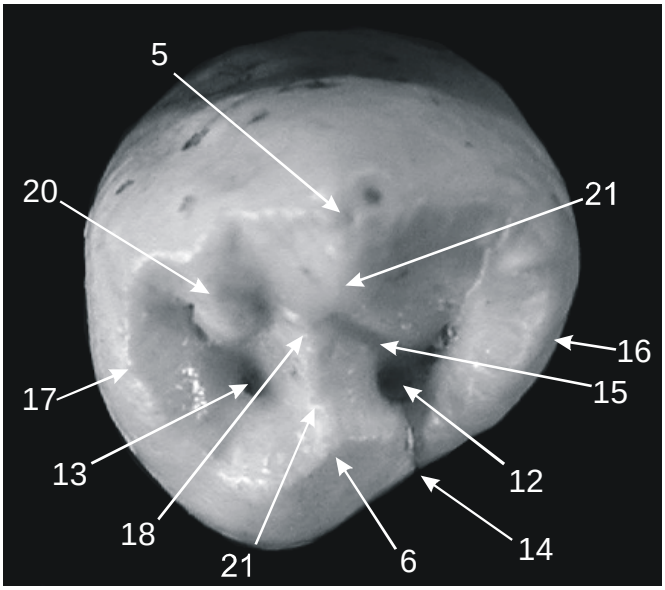
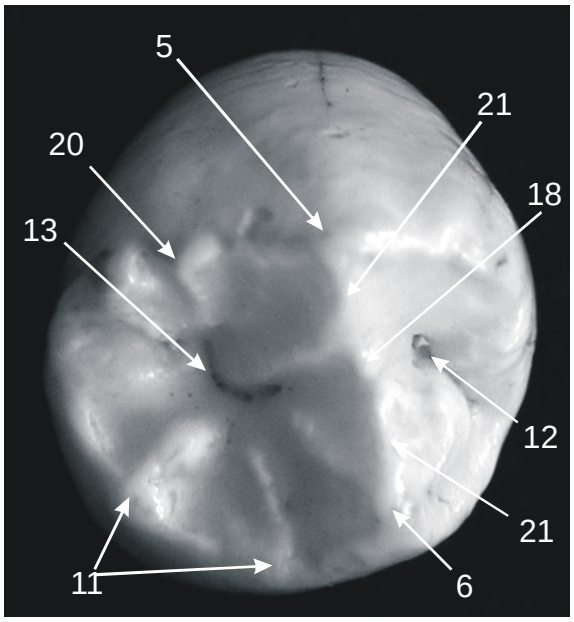


Fig. 4.1. Basic dental terminology used in the text

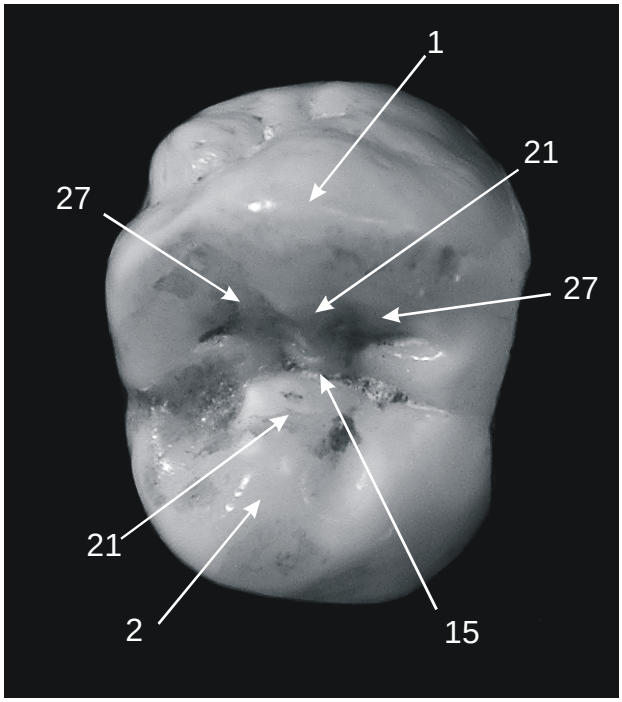


a.

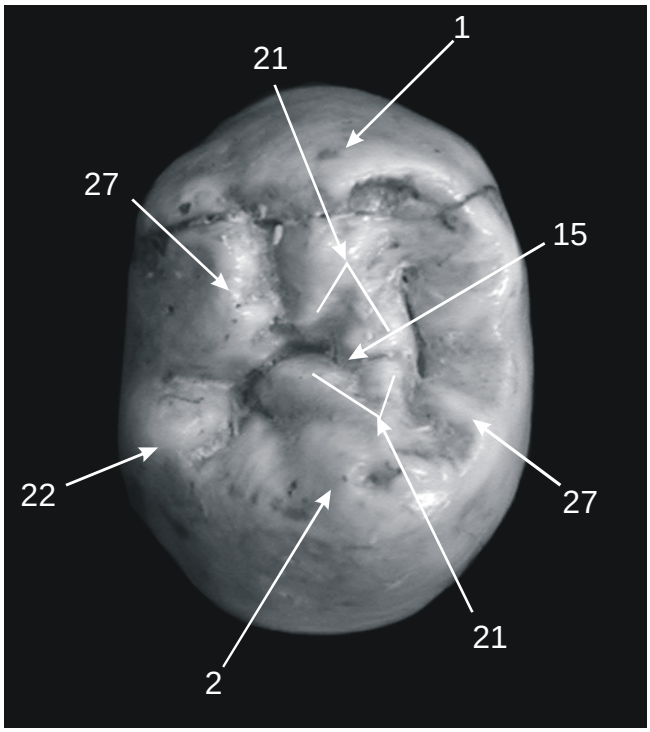


b.

Fig. 4.2. Elements of the mandibular premolar tooth crown referred to in the text. See Table 4.1. a: P_3 (left), b: P_4 (left)



a.



b.

Fig. 4.3. Elements of the maxillary premolar tooth crown referred to in the text. See Table 4.1. a: P^3 (left), b: P^4 (left). Note: The essential crest (21) shown here is bifurcated.

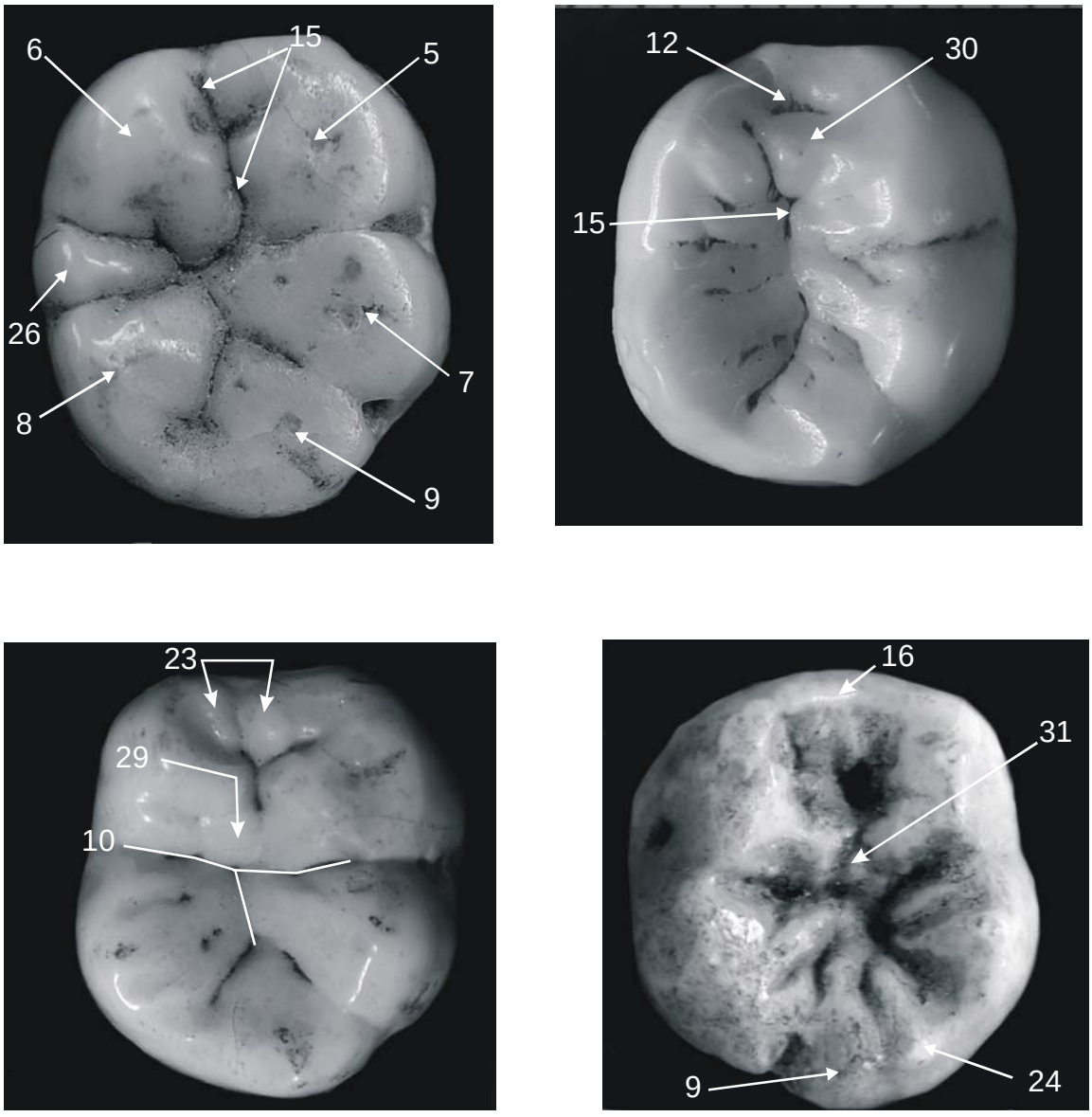


Fig. 4.4. Elements of the mandibular molar tooth crown referred to in the text (right side). See Table 4.1.

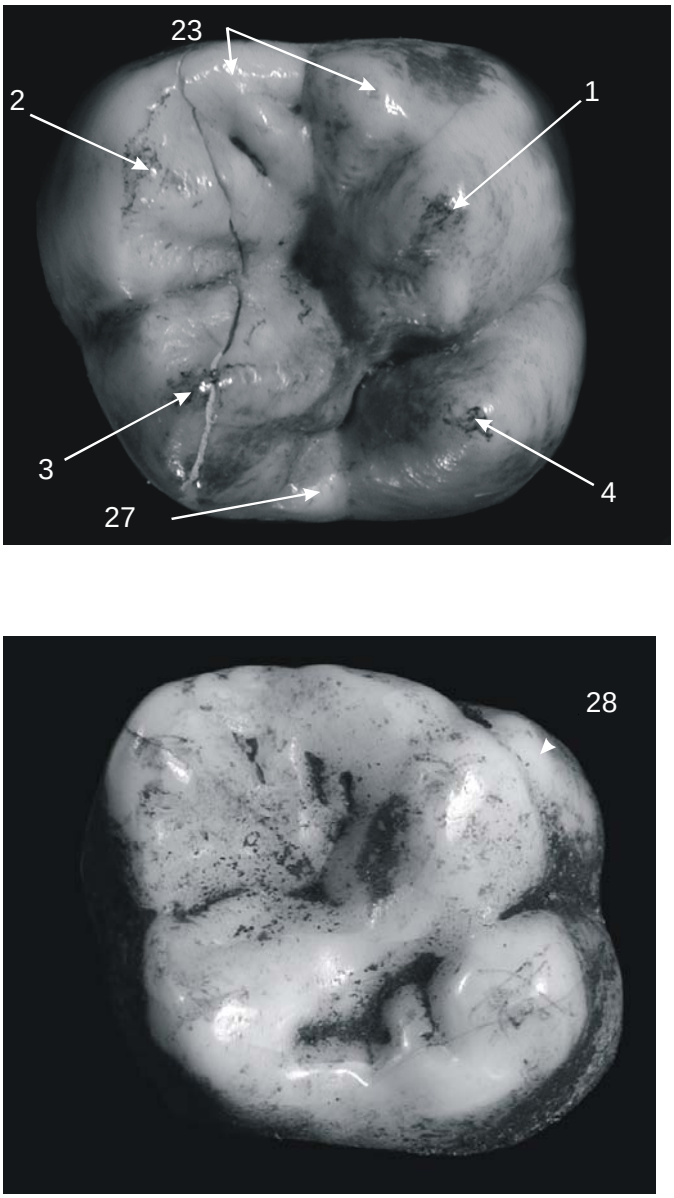


Fig. 4.5. Elements of the maxillary molar tooth crown referred to in the text (left). See Table 4.1.

TABLE 4.2. Dental features/key tooth type used in analysis and abbreviations used in text and tables

Feature	Key tooth type	Abbreviation
Buccal essential crest	Upper premolars	BEC P^3, P^4
Lingual essential crest	Upper premolars	LEC P^3, P^4
Buccal essential crest form	Upper premolars	BECF P^3, P^4
Lingual essential crest form	Upper premolars	LECF P^3, P^4
Buccal maxillary premolar accessory ridges	Upper premolars	BMxPAR P^3, P^4
Lingual maxillary premolar accessory ridges	Upper premolars	LMxPAR P^4
Mesial accessory cusp	Upper premolars	MAC P^4
Distal accessory cusp	Upper premolars	DAC P^4
Hypocone	Upper second molars	HYP M^2
Cusp 5	Upper first molars	C5 M^1
Carabelli's trait	Upper first molars	CARA M^1
Mesial accessory tubercle	Upper second molars	MAT M^2
Mesial lingual groove	Lower first premolars	MLG P_3
Lingual cusp number	Lower second premolars	PLC P_4
Metaconid position	Lower second premolars	METPOS P_4
Transverse crest	Lower second premolars	TRC P_4
Distal accessory ridge	Lower second premolars	DAR P_4
Mesial accessory ridge	Lower second premolars	MAR P_4
Crown asymmetry	Lower second premolars	P_4 ASM
Groove pattern	Lower second molars	YPAT M_2
Cusp number	Lower second molars	4CSP M_2
Deflecting wrinkle	Lower first molars	DW M_1
Distal trigonid crest	Lower first molars	DTC M_1
Mid-trigonid crest	Lower first and second molars	MTC M_1 or M_2
Mesial marginal ridge	Lower first and second molars	MMR M_1 or M_2
Anterior fovea	Lower first molars	AFOV M_1
Cusp 6	Lower first molars	C6 M_1
Cusp 7	Lower first molars	C7 M_1

Data collection

While the use of as many key tooth traits as possible would be most desirable, post-mortem tooth loss and excessive occlusal attrition led to variably sized data sets. To maximize sample sizes, all dentitions and isolated teeth from fossils that preserved at least some morphology were scored and analyzed. Dentitions of contemporary humans were scored and analyzed if they were relatively unworn [grade 0 (no wear) to grade 1 (dentin exposed on one or more cusps)] and preserved at least one of each tooth group on either the left or right side. However, in some cases assessment of trait's presence could be ascertained even when the tooth was quite worn (e.g., P_4 transverse crest). Although tooth wear creates problems for obtaining all kinds of metric and morphological data, angular variables and intercuspal distances are particularly susceptible to error when a tooth is worn. Therefore, these metric variables were only recorded on relatively unworn teeth. While this significantly reduced sample sizes, more meaningful data were obtained as a result.

Trait frequencies were derived using the individual count method (Scott and Turner, 1988). This method involves scoring both right and left sides of the dentition but only uses the side with the highest trait expression in the analysis. The rationale for this method is both statistical and genetic. Statistically speaking, using both sides of the dentition and analyzing them separately can lead to inflated sample sizes; conversely, focusing on only the right or left side results in a considerable data loss (especially in fossil samples). Genetically speaking, using both sides of the dentition and analyzing

them separately assumes that an individual has two separate genotypes for a particular trait, which does not seem likely.

Asymmetry in non-metric traits is likely attributable to developmental noise and/or environmental factors (Di Bennardo and Bailit, 1978; Doyle and Johnston, 1977; Perzigian, 1977; Potter and Nance, 1976; Trinkaus, 1978a) and is not necessarily an indication of heterozygosity (Searle, 1954). As such, it seems logical to presume that the tooth with the greatest degree of trait expression represents the underlying genotype for a particular individual. This assumes that environmental factors act to suppress rather than enhance morphological expression – an assumption that is supported by studies showing that morphological features appearing on the dentin surface sometimes do not appear on the enamel surface (Korenhof, 1960; 1961). In such cases, the trait has been obscured by extra enamel. In any case, trait frequencies obtained from different counting methods are nearly identical and the particular counting method employed does not appear to have a significant impact on results (Scott, 1980).

Non-metric data

The Arizona State University dental anthropology system

The Arizona State University Dental Anthropology System (ASUDAS) served as the starting point for collecting non-metric dental data. Although published little more than a decade ago (Turner et al., 1991), the ASUDAS has its roots in standards developed almost 40 years before by A. A. Dahlberg (1956). This system currently consists of more than 36 tooth crown and root traits that are scored with the aid of 23 reference plaques (Turner et al., 1991). A written description of each trait is used in conjunction

with reference plaques to facilitate accurate assessment of variation. Descriptions of these traits along with dichotomized presence/absence breakpoints are provided in Appendix A and the standard form used to record variation for each individual is reproduced as Appendix B.

Because many of the ASUDAS crown traits are scored on multiple teeth (e.g., M^1, M^2, and M^3) within a tooth field (incisors, canines, premolars, molars), and because the ASUDAS includes morphological characters on the tooth roots, the cranium and mandible (tori and rocker jaw), as well as the presence of supernumerary teeth, there are potentially a very large number (> 300) of observations that could be made on each individual. Turner (1987) indicated that of these, 29 features best characterize genetic affinity. These 29 traits are least likely to be strongly influenced by environment when scored on "key" teeth as defined by the morphogenetic field concept (Dahlberg, 1945). As the focus of this study is on the postcanine teeth, only 20 of the ASUDAS traits were used in the analysis. Expression of each trait was scored on each tooth in the morphological field, but only the expression on the key tooth (see Table 4.2) was used in the analysis.

A supplemental scoring system

The ASUDAS is based on recent modern human variation and was developed for the purpose of comparing intraspecific variation in *Homo sapiens* populations of contemporary origin. By design, it includes only those dental traits that are present and morphologically variable in recent and contemporary human populations. To determine whether this system could be applied to fossil hominids generally and to Neandertals

specifically, I undertook two pilot studies. The first included an analysis of dental casts of Krapina Neandertal teeth from Dr. Erik Trinkaus's collection at Washington University, St. Louis. The results of that study indicated that much, but not all, of the variation observed in Neandertal teeth could be captured by the ASUDAS. Several studies have since confirmed that the ASUDAS can be used effectively in phenetic distance analyses of both Neandertal and contemporary modern human dentitions (Bailey, 2000b; Bailey and Turner, 1999; Coppa et al., 2001; Irish, 1998). In addition to confirming results of the first study, the second pilot study – which included Near East Neandertals as well as Upper Paleolithic amHs – indicated that some potentially important dental crown characters found in Neandertals were not included in the ASUDAS. Therefore, while the ASUDAS is a good place to start, it is (by its very nature) biased in that only those characters that are present and variable in modern humans are evaluated. Characters that are present but invariable or absent in modern humans are not included in the system, as they would not be useful for the purpose for which it was designed.

Following the first pilot study, I developed preliminary dental plaques to visually represent some of the new (non-ASUDAS) characters I had observed. I then conducted a literature search to compile a list of additional dental characters that might be important in studies of pre-modern dentitions. This literature review focused primarily on Patte's (1959) study of the Neandertal dentition, Wood et al.'s and Suwa's studies of Plio-Pleistocene hominid postcanine dental variation (Suwa, 1991; Wood and Abbott, 1983; Wood et al., 1983; Wood and Engleman, 1988; Wood and Uytterschaut, 1987) and on

studies of human premolar variation (Genet-Varcin, 1962; Kraus and Furr, 1953; Ludwig, 1957). Both the pilot studies and the literature review confirmed that much of the variation present in fossil hominids but not accounted for by the ASUDAS could be found in the postcanine teeth, especially in the maxillary and mandibular premolars. In the end I chose 22 traits – many of which describe premolar variation – to supplement the ASUDAS. Descriptions of these traits along with dichotomized presence/absence breakpoints are provided in Appendix C. The form on which variation was recorded is reproduced in Appendix D.

Metric data

Occlusal digital photographs

The procedures for taking occlusal photographs were as follows:

1) I used a Nikon CoolPix™ 950 digital camera to capture images of the occlusal surfaces of the teeth. The camera was attached to a tripod and was leveled horizontally and vertically. All pictures were taken with the macro camera setting using the smallest aperture available, which provided the highest depth of field.

2) Loose teeth were mounted on modeling clay and each tooth was positioned so that its occlusal plane was perpendicular to the visual (vertical) axis of the camera lens. For teeth *in situ*, the cranium or mandible was manipulated so that the occlusal surface of the particular tooth was perpendicular to the optical axis of the camera. A millimeter scale was included in each photograph for later calibration.

Tooth measurements

All data processing was conducted using an IBM compatible personal computer. I used the program SigmaScan® Pro 5.0 (©SPSS, Inc.) to take linear, angular and area measurements from the occlusal photographs. This program allowed me to calibrate photographs and measurements directly from the scale placed in the photograph next to the tooth of interest. Photographs were cropped and rotated so that the tooth of interest was oriented with its mesio-distal axis parallel to the base of the photograph (the x axis). To ensure that the angle of the scale did not affect calibration the scale was oriented vertically with respect to the tooth.

One advantage of using digital photography is that it facilitates correcting for interproximal (IP) wear that would affect measurements. I used the method described in Wood and Abbot (1983) to make corrections in worn teeth. This involved estimating the original mesial and/or distal crown margins as indicated by the overall crown shape and the buccolingual limits of the wear facet(s). Correcting for IP wear was particularly important in this study because, generally speaking, contemporary amHs teeth were (by the process of selection) less worn than those of the fossil hominids. Using uncorrected measurements could have led to differences between samples that were the result of interproximal wear rather than actual differences in tooth size.

The measurements used in this study are illustrated in Figs. 4.6 and 4.7. All measurements were rounded to the nearest tenth of a millimeter. Individual cusp areas were measured by tracing along the primary fissures that separate them making necessary corrections for interproximal tooth wear. Where accessory cusps were present (e.g., C6

or C7), the area of the accessory cusp was divided between the adjacent main cusps in the manner described by Wood and Abbott (1983). The cusp areas were then added together to calculate the total crown base area. Relative cusp areas were computed by expressing the actual cusp area as a percentage of the measured crown base area.

The samples used to estimate cusp angles, intercuspal distances and the occlusal polygon area (the area described by connecting the tips of each cusp) were smaller than other samples because only those teeth that exhibited minimal wear (dentin exposed on not more than one cusp) could be included. In the case where some dentin was exposed on a particular cusp, the intercuspal distances were taken from the center of the exposed dentin. Cusp angles, intercuspal distances and occlusal polygon areas were automatically calculated using SigmaScan® Pro's measurement mode. Relative occlusal polygon areas were then calculated by expressing the occlusal polygon area as a percentage of the measured crown base area.

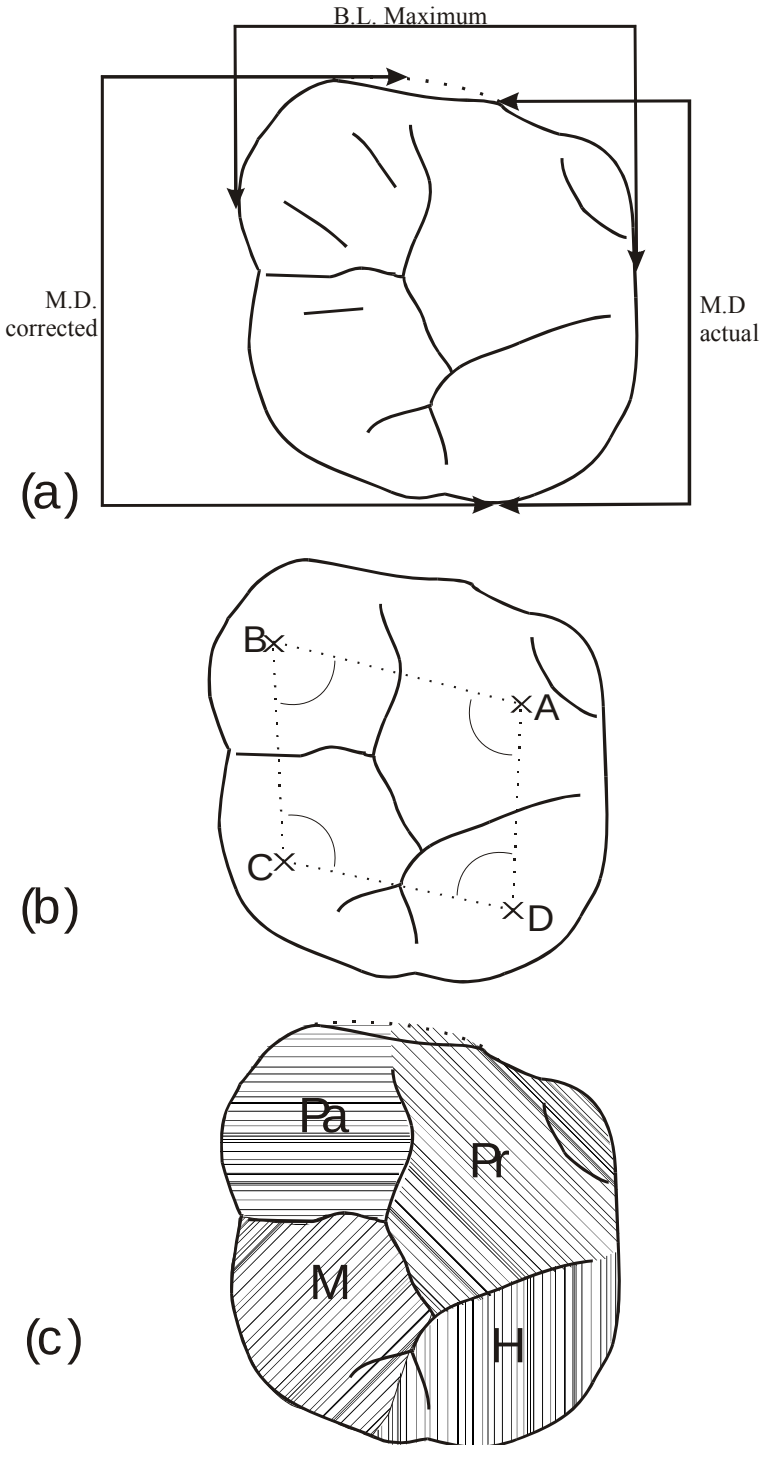


Fig. 4.6. Diagrams showing linear measurements (a), cusp angles (b) and measured areas of major cusp components of the maxillary molar (right).

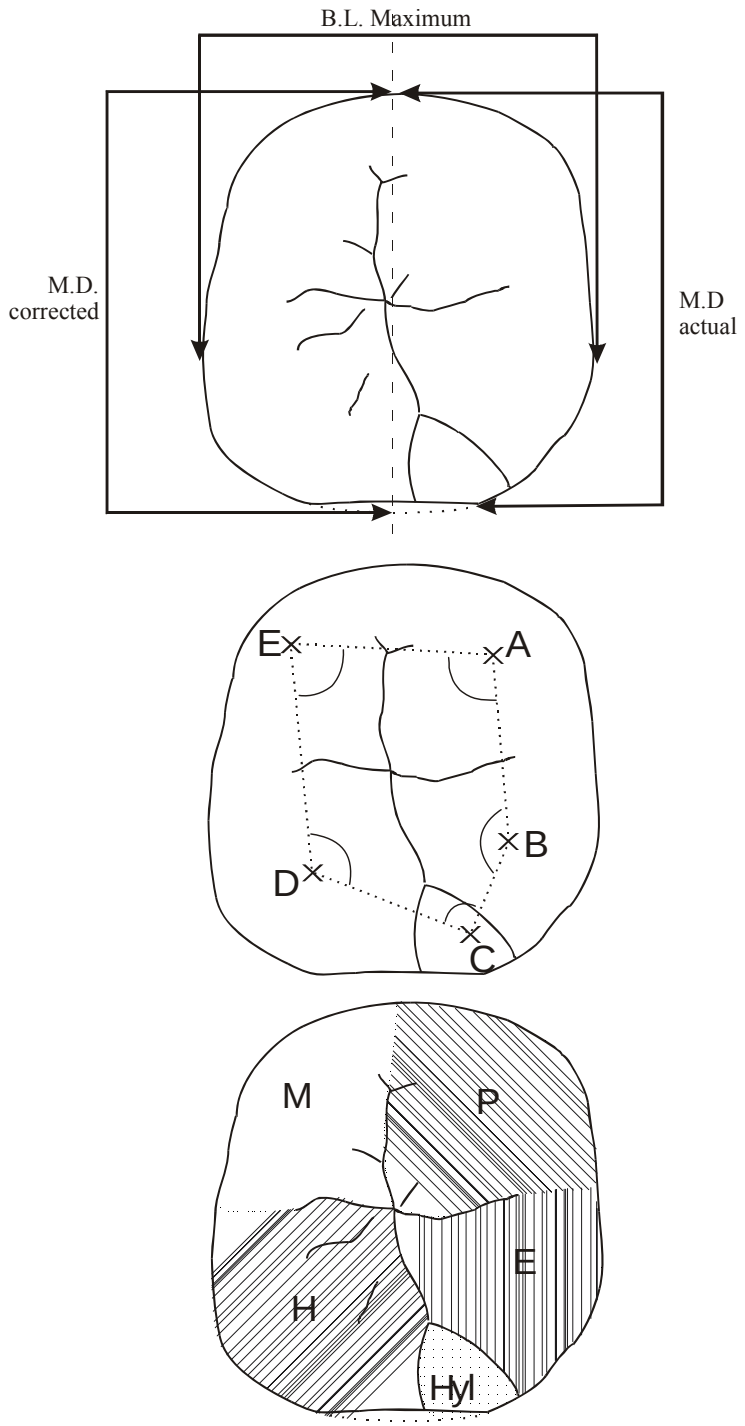


Fig. 4.7. Diagrams showing linear measurements (a), cusp angles (b) and measured areas of major cusp components of the mandibular molar (right).

TABLE 4.3. Description of metric variables. Refer to Figs., as noted

Variable	Tooth	Description
Linear		
mesiodistal length (corrected)	P_4, molars	maximum distance between the mesial and distal crown margins, taken parallel to the longitudinal axis (central groove) corrected for interproximal wear
buccolingual breadth (BL)	P_4, molars	maximum distance between the buccal and lingual crown margins, taken perpendicular to the MD length
Crown area		
measured crown area	P_4, molars	taken from perimeter of tooth (corrected for interproximal wear)
occlusal polygon area	molars	area enclosed by cusp tips (max: area ABCD; mand: area ABCDE, see Figs. 4.6, 4.7)
Crown component area		
protocone (Pr) area	molars	See Fig. 4.6
paracone (Pa) area	molars	See Fig. 4.6
metacone (M) area	molars	See Fig. 4.6
hypocone (H) area	molars	See Fig. 4.6
protoconid (P) area	molars	See Fig. 4.7
metaconid (M) area	molars	See Fig. 4.7
hypoconid (H) area	molars	See Fig. 4.7
entoconid (E) area	molars	See Fig. 4.7
hypoconulid (Hyl) area	molars	See Fig. 4.7
Angular variables		
A, B, C, D	molars	See Fig. 4.6
A, B, C, D, E	molars	See Fig. 4.7
Indices/ratios		
Relative cusp area	molars	Individual cusp area/measured crown area
Relative occlusal polygon area	molars	occlusal polygon area/measured crown area

Justification of methodology and measurement error

Understandably, there is some concern about the validity of taking measurements of a three-dimensional object on a two-dimensional photograph. To address this issue I conducted two tests of measurement error. The first test compared measurements taken with a point digitizer, digital calipers and from occlusal photographs; the second test compared area measurements of the same tooth taken directly from digital occlusal photographs at different times. The first test addressed intraobserver error and error attributable to different methodology, while the second addressed intraobserver error due to calibration.

To address the first type of error I compared measurements taken on five upper and five lower molars casts from the Krapina Neandertal sample. Overall, the results indicate that measurements taken from digital occlusal photographs are very similar to those using calipers or the point digitizer (see Tables 4.4 and 4.5). In addition to the finding that measurements taken from a two-dimensional method are within the ranges of those obtained through three-dimensional methods, I found no consistent pattern regarding the nature of measurement error. For example, occlusal polygon and angular measurements taken from digital photographs were not consistently higher or lower than those obtained from three-dimensional means. Paired t-tests revealed a significant difference for only one linear measurement (DE: distance between metaconid and entoconid). Occasionally, I encountered unusually high measurement error exceeding 10%. This is most likely attributable to moderate wear on one of the tooth cusps.

TABLE 4.4. Error ranges and average error values for intercuspal measurements of Krapina molars

Source of Error	Range across variables	Average all variables
Upper Molars (n=5)		
Intraobserver (using point digitizer)	.3-.5 mm	.32 mm
Caliper vs digitizer (both 3D methods)	.2-.5 mm	.31 mm
Calipers vs. digital photo (3D vs. 2D)	.2-.6 mm	.34 mm
Lower Molars (n=5)		
Intraobserver (using point digitizer)	.3-1.7 mm	.5 mm
Caliper vs digitizer (both 3D methods)	.1-.8 mm	.5 mm
Calipers vs. digital photo (3D vs. 2D)	.1-1.5 mm	.8 mm

TABLE 4.5. Error ranges and average error values for cusp angle measurements of Krapina molars (in degrees)

Source of Error	Range across variables	Average all variables
Upper Molars (n=5)		
Intraobserver (using point digitizer)	1.3-7.0	3.5
Calipers vs. digital photo (3D vs. 2D)	1.4-4.7	3.5
Lower Molars (n=5)		
Intraobserver (using point digitizer)	2.1-4.6	3.5
Calipers vs. digital photo (3D vs. 2D)	1.0-5.9	2.9

When examined on a variable-by-variable basis the data indicate that no one variable incurred greater measurement error than any other. The data do suggest that there may be a tendency for the *average* error rate using digital photographs to be higher than intraobserver error. However, this is not a consistent pattern. Instead, the percentage error for two-dimensional vs. three-dimensional methods is most often within the range of error obtained when the same method or different three-dimensional methods are used (see Table 4.6).

TABLE 4.6. Summary of measurement error for intercuspal measurements (refer to Figs. 4.6 and 4.7)

	Lower Molars			Upper Molars		
Measurement Error type	Range %	Mean %	SD %	Range %	Mean %	SD %
AB						
Intraobserver (point digitizer)	0.3-8.9	4.6	3.6	2.2-7.7	4.7	2.9
Calipers vs. point digitizer (3D vs. 3D)	2.8-8.5	5.1	2.3	0.9-11.5	4.8	4.5
Calipers vs. digital photo (3D vs. 2D)	1.6-18.1	9.8	5.9	1.3-8.0	3.5	2.7
AC						
Intraobserver (point digitizer)	0.1-8.6	4.7	3.5	1.8-17.1	7.3	5.9
Calipers vs. point digitizer (3D vs. 3D)	0.1-8.3	3.7	3.5	0.5-14.6	6.2	6.0
Calipers vs. digital photo (3D vs. 2D)	0.9-7.8	4.5	2.5	0.5-27.3	8.5	10.7
AD						
Intraobserver (point digitizer)	1.0-4.9	2.3	2.0	0.8-12.8	5.2	4.7
Calipers vs. point digitizer (3D vs. 3D)	1.0-5.8	3.4	2.2	0.8-16.8	7.3	5.9
Calipers vs. digital photo (3D vs. 2D)	0.2-7.6	4.0	2.8	1.7-16.6	9.9	6.0
AE						
Intraobserver (point digitizer)	0.8-5.7	4.8	4.5			
Calipers vs. point digitizer (3D vs. 3D)	1.8-12.4	4.7	4.3			
Calipers vs. digital photo (3D vs. 2D)	2.4-13.3	7.8	4.1			
BC						
Intraobserver (point digitizer)	0.5-7.3	3.5	2.8	4.2-10.0	6.4	2.4
Calipers vs. point digitizer (3D vs. 3D)	2.3-16.0	10.3	6.8	0.3-11.3	4.3	4.9
Calipers vs. digital photo (3D vs. 2D)	2.5-14.8	7.8	4.8	0.9-11.4	3.6	4.4
BD						
Intraobserver (point digitizer)	2.6-11.2	6.8	3.6	0.5-7.8	2.6	2.9
Calipers vs. point digitizer (3D vs. 3D)	0.8-5.2	2.7	1.8	0.3-5.1	1.5	2.0
Calipers vs. digital photo (3D vs. 2D)	0.9-5.0	1.6	2.3	0.8-2.7	1.4	0.7
BE						
Intraobserver (point digitizer)	0.0-2.3	1.3	1.0			
Calipers vs. point digitizer (3D vs. 3D)	0.8-8.5	2.6	3.3			
Calipers vs. digital photo (3D vs. 2D)	8.1-10.5	6.4	3.5			
CD						
Intraobserver (point digitizer)	1.5-12.6	7.0	5.6	1.7-7.9	4.0	2.5
Calipers vs. point digitizer (3D vs. 3D)	2.7-14.3	6.8	4.4	1.0-10.8	4.9	4.1
Calipers vs. digital photo (3D vs. 2D)	3.2-15.6	8.8	6.1	0.4-14.0	5.5	5.8
CE						
Intraobserver (point digitizer)	0.1-4.8	2.0	2.2			
Calipers vs. point digitizer (3D vs. 3D)	0.2-10.2	3.2	4.1			
Calipers vs. digital photo (3D vs. 2D)	2.0-9.9	4.5	3.2			
DE						
Intraobserver (point digitizer)	0.0-2.7	1.6	1.3			
Calipers vs. point digitizer (3D vs. 3D)	0.5-5.9	3.0	2.2			
Calipers vs. digital photo (3D vs. 2D)	3.0-13.6	7.7	5.0			

The second test of measurement error involved analyzing the error attributable to differences in calibration. To test the degree of error, duplicate measurements of cusp areas and crown base areas were taken on a subsample (n=10) of contemporary modern human maxillary molars on two separate occasions, taking new calibrations each time. The measurement error ranged between 0% and 4% and averaged 2%. To correct for this kind of error all measurements were calibrated three times and the average of the three was used in the analysis.

Occlusal photographs make it possible to gather accurate information on tooth crown and cusp areas that are not possible using digital calipers (Wood and Abbott, 1983; Wood et al., 1983; Wood and Engleman, 1988; Wood and Uytterschaut, 1987). While there is certainly error inherent to using this methodology, I believe it is safe to assume that measurements taken from digital occlusal photographs accurately represent the parameters of interest to this study. Basic crown measurements (BL, MD and intercuspal distances) of all teeth were also taken with digital calipers as a back up reference.

Morphometric analysis

Because of the asymmetry noted in the occlusal outline of Neandertal mandibular premolars I undertook a morphometric analysis of its crown shape. The data acquisition program TPSdig (Rohlf, 2001) was used to produce coefficients describing the outline of each tooth. Each tooth was oriented as close to its natural position as possible, such that its mesio-distal axis ran parallel to the base of the photograph (X axis). The left side was chosen arbitrarily for analysis, and photographs of teeth from the right side of the jaw were flipped horizontally so that they represented the left side. Only one tooth (the best

preserved tooth or least worn) was used from each individual. Differences in tooth size were not an issue, as the program automatically eliminated the effect of size on the shapes. The "find contour" option was used to trace the contour and obtain coordinates describing the tooth's shape. The morphometric analysis program Morpheus (Slice, 2000) was then used to run Elliptic Fourier Analysis (EFA) on the data. Output from EFA included a plot of the average tooth shape for each group and EFA coefficients for each individual. These coefficients were then used in principal components and discriminant function analyses.

Statistical procedures

Phenetic analysis

I carried out all statistical analyses on an IBM-compatible personal computer using the Statistica (© Statsoft, Inc.) software package. Descriptive statistics (mean, standard deviation, range) were calculated for tooth crown areas, relative cusp areas, and relative occlusal polygon areas, as well as for cusp angles and crown indices in each comparative sample, where relevant. Descriptive statistics were also calculated for morphometric data (e.g., cusp angles and occlusal polygon areas). Differences in metric variables, such as cusp angles, reflect differences in the cusp configuration and overall shape of the tooth crown. The results of descriptive statistics provided an initial assessment of group differences.

The question of Neandertal uniqueness (Hypothesis 1) was tested using both metric and morphological characters. Analysis of metric variables consisted of conducting significance tests of group means. In most analyses sample sizes were small

and it was not possible to obtain a normal distribution of the data. Therefore I applied non-parametric tests of group means (Kruskal-Wallis) to the data. If any of these tests revealed significant differences, further analyses were conducted. In these cases, I used the Mann-Whitney U test to ascertain which groups contributed to differences observed.

In addition, I conducted principal component and discriminant function analyses on subsets of the metric variables to summarize inter- and intra- sample variation without *a priori* grouping of specimens. The distribution of specimens along different principal components was useful for identifying significant sources of variation between groups.

The existence and nature of Neandertal dental uniqueness was also assessed using non-metric variables. Dental trait frequencies were obtained for all samples. The combination of low and high trait frequencies was then used to construct a Neandertal dental morphological pattern. After these metric and non-metric analyses were complete characters that showed potential for separating taxonomic groups were further quantified into character states for cladistic analyses (see below).

Neandertal affinities

To test hypotheses about phenetic affinities, distance statistics using multivariate analyses such as CAB Smith's (in Berry and Berry, 1967) mean measure of divergence analysis (MMD) were used to assess biological relationships between fossil and contemporary human groups. Mean Measure of Divergence analysis provides a measure of phenetic similarity based on the entire suite of dental traits. Divergence between two samples was considered significant at the .025 level of probability when the MMD is greater than twice the standard deviation (Sjøvold, 1973). Cluster analysis using Ward's

method was used to visually represent similarity among samples following MMD analysis.

Neandertal affinity was also assessed using cladistic analyses. This analysis was based on weighted trait frequencies (Turner, 1985) as opposed to unweighted frequencies (e.g., Stringer et al., 1997), which requires dichotomizing quasi-continuous variation into presence and absence states. Unweighted trait frequencies ignore information about trait expression, as any degree of expression that exceeds the established breakpoint is counted as present (e.g., grade 1 M^1 Cusp 5 is treated the same as grade 5 M^1 Cusp 5). Weighted trait frequencies, on the other hand, convey information about trait expression. It is conceivable, if not likely, that group differences in trait *expression* (not just presence) could convey important information.

To obtain a weighted trait frequency for a particular trait, the trait frequency for each grade is multiplied by the assigned coefficient and the results are then summed into a single frequency value. Coefficients are derived by dividing 1.0 by the total number of grades, and then multiplying that number by the particular grade. For example, a trait that has four grades of presence (e.g., I^1 labial convexity) would have a coefficient for grade 1 equal to 0.25, for grade 2 , 0.50, for grade 3, 0.75, and for grade 4, 1.0. If 100% of a population exhibits grade 4 labial convexity, the population's frequency for that trait would be 100%. If, on the other hand, 50% of the population exhibits grade 1 labial convexity, and 50% of the population exhibits grade 2 labial convexity the population's frequency for that trait would be

0.50*0.25 + 0.50*0.50, or 0.375.

The underlying assumption of this method is that dental traits are inherited according to a polygenic additive model. One advantage of this method is that expression counting based on weighted frequencies increases the chances that a small sample will be representative of the actual population frequency of a particular trait (Turner, 1985).

One of the strengths of using dental traits in phenetic analyses of contemporary humans is that the traits are intraspecifically variable, and as such are very useful in working out biological relationships among geographically defined populations. Characters selected for cladistic analyses, on the other hand, typically consist of those that are not highly variable intraspecifically. One way to resolve this dilemma is to treat dental trait frequencies as continuous variables and to use a method designed to handle quantitative data for the analysis. These methods (e.g., simple gap coding, generalized gap coding, segment coding and gap weighting) involve coding continuous metric variation into discrete character states. Of these, gap weighting (Thiele, 1993) seems to be the quite promising and it has been recently applied to cladistic analyses of contemporary humans using the same type of data (Stringer et al., 1997). One advantage to Thiele's method is that it preserves information on the size of gaps between the states and differentially weights these gaps according to their size (larger gaps are weighted more heavily than smaller gaps). The computer program used is the only factor that limits the number of states that the quantitative information can be partitioned into.

The programs PAUP™ 4.0 [Phylogenetic Analysis Using Parsimony: Swofford (1996)] and MacClade 4.0 (Maddison and Maddison, 2000) were used to generate and evaluate different cladograms from the dental trait frequencies.

POSTCANINE DENTAL MORPHOLOGY AND MORPHOMETRICS

Compared to the efforts made to understand the nature and distribution of incisor variation in Mid-Late Pleistocene humans, it seems that much of the morphological variation in the postcanine teeth in these fossil hominids has been overlooked. Although some have described (e.g., Genet-Varcin, 1962; Leroi-Gourhan, 1958; Patte, 1959) or alluded to (Tattersall and Schwartz, 1999) potentially diagnostic postcanine dental characters in Neandertals, little effort has been made to characterize this variation.

This chapter systematically compares Neandertal postcanine dental morphology and morphometrics with that of *Homo erectus*, archaic *Homo sapiens* and anatomically modern *Homo sapiens*. The morphological section has several goals: (1) to provide a tooth-by-tooth description of Neandertal postcanine teeth; (2) to compare trait frequencies among the sampled groups to determine for which traits, and in what ways, the Neandertal dentition differs from other groups; and (3) to ascertain whether any of these characters are uniquely derived in Neandertals (i.e., they do not exist in other groups). These assessments will make it possible to formally outline the traits and trait frequencies that contribute to the Neandertal dental pattern.

Because some dental characters, such as tooth shape (molars) and tooth asymmetry (P_4), can be described morphometrically, the morphological study is followed by a morphometric study of these characters. With the same goals of the morphological study in mind, the morphometric portion uses univariate and multivariate statistical methods to test the significance of some of the tooth shape differences observed in Neandertals.

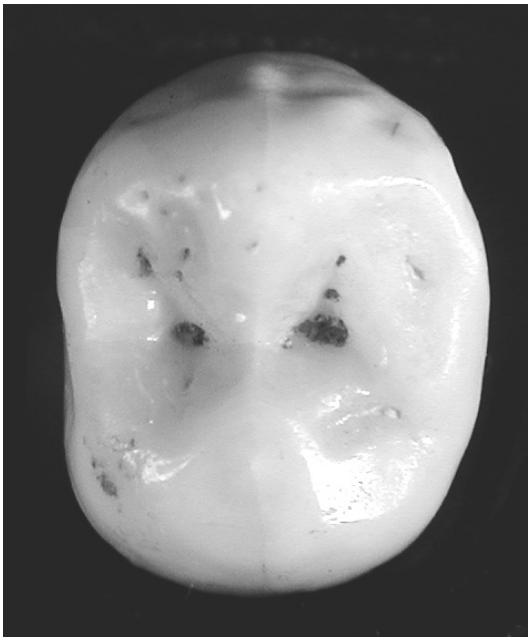
Morphology

Maxillary premolars

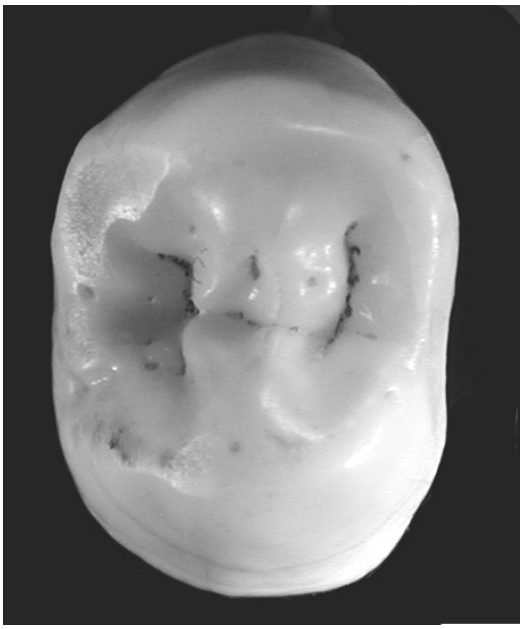
Description

Neandertal maxillary premolars are relatively constant in form and occlusal morphology (Fig. 5.1). The two primary cusps (protocone and paracone) are marked by the presence of a strong essential crest. In addition, both P^3 and P^4 tend to express mesial and distal accessory ridges and accessory cusplets. Traits such as the distosagittal ridge, tricuspid premolars and odontomes that are rare in contemporary amHs (Morris et al., 1978) were not observed in Neandertals nor in other fossil hominids included in this study.

The mesial and distal accessory cusps noted above are fairly common. They occur more frequently on P^3 than on P^4 and are found more often distally than mesially (63.2% vs. 36.8% on P^3 and 38.9% vs. 18.8% on P^4). Maxillary premolar accessory ridges (MxPAR) are also common but occur more often on P^4 than on P^3 (85.7% vs. 68.8%, respectively). Moreover, they tend to occur more often on the protocone than the paracone (68.8% vs. 46.7% in P^3 and 85.7% vs. 60% on P^4). While the essential crest of both the protocone and paracone is well developed in all cases, its form varies – it may be a single ridge (as in Fig 5.11[a]) or it may be bifurcated (as in Fig 5.11[b]). The bifurcated ridge has been called the "triangular ridge bifurcation" by Burnett [1998]). This form of the essential ridge is fairly frequent in Neandertals. It occurs on the protocone of both P^3 and P^4 in approximately equal frequencies (62.5% and



a.



b.

Fig. 5.1. Neandertal maxillary premolars: a) left P^3 b) right P^4

66.7%, respectively) but is more prevalent on the paracone cusp of P3 than on P4 (57.1% vs. 46.7% respectively).

Overall, it is difficult to say which of the two teeth (P^3 or P^4) is more complex morphologically as P^3 exhibits accessory cusplets more often than P^4, but P^4 exhibits accessory ridges more often than P^3. It does appear, however, that both teeth exhibit greater complexity buccally and/or distally than they do lingually and/or mesially.

Morphologically, there is little else to note about Neandertal maxillary premolars. Some researchers have suggested that morphometric analyses of maxillary premolar shape, such as cusp angles (Morris, 1981) and shape expressed in terms of landmark data (Lavelle, 1984) have discriminatory power among contemporary amHs. Whether these morphometric traits have discriminatory power among fossil hominids was not tested here because there was no obvious indication that Neandertals and amHs differ in these characters.

Comparison

Tables 5.1 and 5.2 present the trait frequency comparisons among Neandertals, fossil and contemporary human groups. In general, Neandertal maxillary premolar trait frequencies are most similar to those observed in other fossil hominids (see Figs. 5.2 and 5.3). Contemporary amHs, on the other hand, show a tendency toward simplification of the occlusal surface.

TABLE 5.1. A comparison of P^3 trait frequencies

	BEC[1]		LEC		BECF		LECF		BMxPAR		LMxPAR		DAC		MAC	
Samples	N	%[2]	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Homo erectus	3	100	3	66.7	3	66.7	3	33.3	3	66.7	3	33.3	2	0.0	3	0.0
Archaic *Homo sapiens*	3	100	3	100	3	33.3	3	0.0	2	100	1	-	1	-	2	50.0
Neandertals	**16**	**100**	**13**	**100**	**16**	**62.5**	**14**	**57.1**	**16**	**68.8**	**15**	**46.7**	**19**	**63.2**	**19**	**36.8**
Early amHs	2	100	2	100	2	50.0	2	0.0	2	0.0	2	50.0	3	0.0	3	33.3
Upper Paleolithic amHs	2	100	3	100	1	+	2	0.0	1	-	1	-	4	50.0	4	25.0
Cont. amHs (pooled)	117	80.3	116	31.9	115	14.8	114	4.4	108	38.9	112	11.6	121	19.0	124	34.7
North Africa (NAF)	18	72.2	18	38.9	18	11.1	18	5.6	17	35.3	18	11.1	18	11.1	18	22.2
West Africa (WAF)	16	68.8	16	31.3	16	25.0	16	0.0	16	68.8	17	23.5	17	23.5	15	26.7
Northeast Asia (NEAS)	9	88.9	9	22.2	9	33.3	9	11.1	8	75.0	8	12.5	11	18.2	12	75.0
India (IND)	14	100	15	33.3	12	16.7	13	7.7	12	50.0	12	0.0	19	15.8	19	21.1
Near East (WAS)	4	75.0	4	50.0	4	0.0	4	0.0	3	33.3	4	25.0	4	25.0	5	60.0
Europe (EUR)	40	82.5	39	25.6	40	2.5	39	0.0	38	10.5	40	2.5	36	19.4	39	33.3
Australasia (AUST)	16	75.0	15	40.0	16	31.3	15	13.3	14	57.1	13	30.8	16	25.0	16	37.5

[1] Refer to Table 4.2 for trait abbreviations

[2] A "+" indicates that a particular trait was present; a "-" indicates a particular trait was absent from the single individual scored; a * indicates no individuals could be scored for a particular trait.

TABLE 5.2. A comparison of P^4 trait frequencies

	BEC[1]		LEC		BECF		LECF		BMxPAR		LMxPAR		DAC		MAC	
Samples	N	%[2]	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Homo erectus	4	100	2	100	4	50.0	4	75.0	4	75.0	7	50.0	2	0.0	4	50.0
Archaic *Homo sapiens*	2	100	2	100	1	-	1	-	1	-	1	-	1	-	1	-
Neandertals	**18**	**100**	**15**	**100**	**15**	**66.7**	**14**	**85.7**	**14**	**85.7**	**15**	**60.0**	**18**	**38.9**	**16**	**18.8**
Early amHs	2	100	2	100	2	0.0	2	0.0	2	50.0	2	50.0	5	0.0	5	20.0
Upper Paleolithic amHs	3	100	*	*	2	0.0	2	0.0	1	+	*	*	3	33.3	3	0.0
Cont. amHs (pooled)	121	92.6	115	29.6	120	10.0	114	3.5	119	67.2	116	17.2	118	31.4	113	39.8
North Africa (NAF)	18	94.4	16	43.8	18	16.7	16	0.0	19	89.5	16	37.5	18	11.1	16	12.5
West Africa (WAF)	15	93.3	14	50.0	14	14.3	14	7.1	15	86.7	14	50.0	13	38.5	13	46.2
Northeast Asia (NEAS)	13	100	12	25.0	13	23.1	11	9.1	11	72.7	12	0.0	11	36.4	12	16.7
India (IND)	14	92.9	14	14.3	13	0.0	12	8.3	14	71.4	14	0.0	16	37.5	14	21.4
Near East (WAS)	3	66.7	3	33.3	3	0.0	3	33.3	3	33.3	3	66.7	3	0.0	3	33.3
Europe (EUR)	38	89.9	40	17.5	40	2.5	41	0.0	38	39.5	40	7.5	38	36.8	34	47.1
Australasia (AUST)	20	95.0	16	43.8	19	15.8	17	0.0	19	84.2	19	11.8	19	31.6	21	71.4

[1] Refer to Table 4.2 for trait abbreviations

[2] A "+" indicates that a particular trait was present; a "-" indicates a particular trait was absent from the single individual scored; a * indicates no individuals could be scored for a particular trait.

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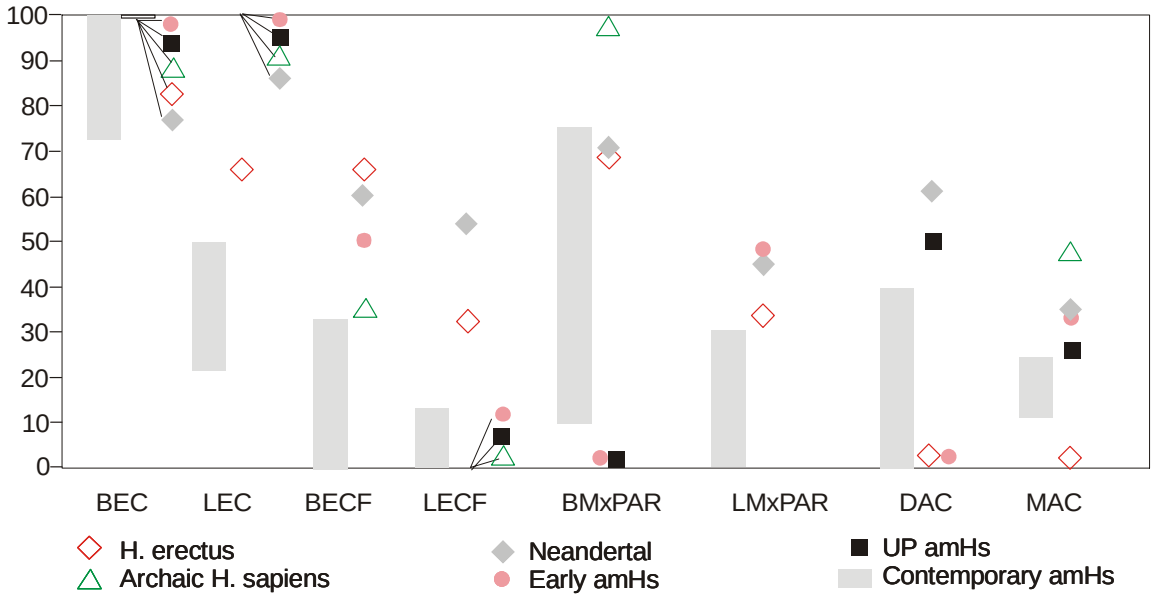


Fig. 5.2. A graphic comparison of P^3 trait frequencies among samples

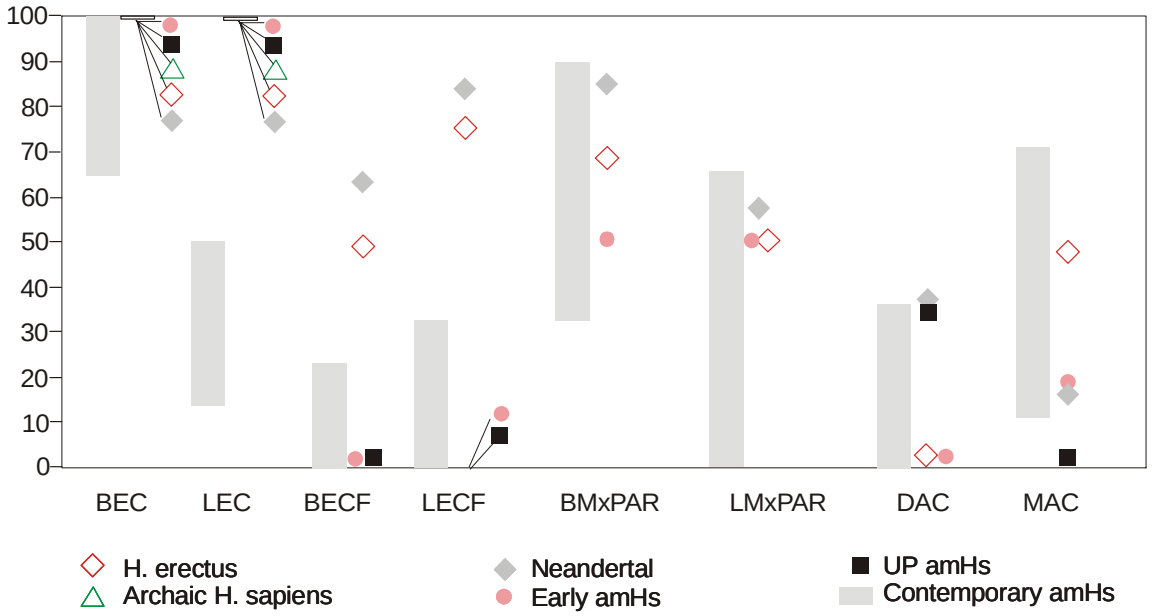


Fig. 5.3. A graphic comparison of P^4 trait frequencies among samples.

A comparison of the maxillary premolar traits among samples follows:

1. Neandertals invariably express a well-developed essential crest (both buccally and lingually). In this respect they are very similar to other fossil hominids. In comparison, contemporary amHs (on average) show somewhat lower frequencies of the essential crest on the protocone (80.3% on P^3 and 92.6% on P^4) and markedly lower frequencies of the essential crest on the paracone (31.9% on P^3 and 29.6% on P^4).
2. Neandertals exhibit high frequencies of a bifurcated essential crest both buccally (62.5% P^3 and 66.7% P^4) and lingually (57.1% P^3 and 85.7% P^4); in fact, their high frequencies lie outside the range observed in contemporary amHs. In comparison, contemporary amHs show much lower frequencies of the bifurcated essential crest on the protocone (14.8% on P^3 and 10% on P^4), and on the paracone its presence is even more rare (4.4% on P^3 and 3.5% on P^4) . In other fossil hominids the bifurcated essential crest occurs more frequently on P^3 than P^4. On P^4 only *Homo erectus* shows a frequency for this trait that is close to that found in Neandertals.
3. Relative to the average frequency found in contemporary amHs (between 11.6% and 67.2% depending on the tooth), Neandertals exhibit high frequencies of MxPAR (P^3 and P^4) both buccally and lingually. However, these frequencies do not fall outside the range observed in contemporary amHs. *Homo erectus* and archaic *Homo sapiens* also tend to exhibit MxPAR, while in the early and Upper Paleolithic amHs samples it is less frequent.

4. Neandertals exhibit moderately high frequencies of mesial and distal accessory cusplets on both P^3 and P^4. These traits are also relatively common in certain fossil hominids and in contemporary amHs. With the exception of the P^3 distal accessory cusplet, the Neandertal frequencies for accessory cusplets fall within the range of contemporary amHs.

Compared to contemporary amHs Neandertals tend to have maxillary premolars that are occlusally more complex. Where sample sizes are large enough, it appears that they are most like other fossil hominids in this regard. In contemporary amHs, P^4 tends to be more complex than P^3, whereas in Neandertals neither tooth could be said to be more complex. As was observed for Neandertals, the lingual surface of contemporary amHs maxillary premolars tends to be less complex than the buccal surface, but in contemporary amHs the difference is more marked than it is in Neandertals. Finally, mesial accessory cusps tend to be more frequent than distal accessory cusps in contemporary amHs, whereas in Neandertals the opposite is true.

As Figs. 5.2 and 5.3 illustrate, most of the variation observed in Neandertal maxillary premolars falls within the ranges of amHs. Exceptions include the frequency of a bifurcated essential crest (both teeth) and the distal accessory cusplet on P^4. However, when compared to other fossil hominids (specifically *Homo erectus*), it is only the bifurcated essential crest on the P^4 paracone and the P^4 distal accessory cusplet that maintain distinctively high frequencies in Neandertals. Thus, morphology alone is not a good tool for distinguishing a Neandertal maxillary premolar from that of other fossil hominids.

Maxillary molars

M^1 description

The Neandertal maxillary first molar is a somewhat crenulated tooth that is characterized by accessory cusps, fissures and crests (Fig. 5.4a). The size of the hypocone is impressive – being larger, on average, than the metacone. Not a single M^1 in my Neandertal sample exhibited hypocone reduction (measured here as ASUDAS grade 3 or less). The M^1s also exhibit high frequencies of Cusp 5 (59%) and Carabelli's cusp (62.5%). Mesial accessory tubercles are fairly common (40%), and usually occur singly rather than as multiple cusplets.

M^1 comparison

Table 5.3 presents the Neandertal M^1 trait frequencies compared to fossil and contemporary anatomically modern humans. A trait-by-trait comparison is summarized below (see Fig. 5.5).

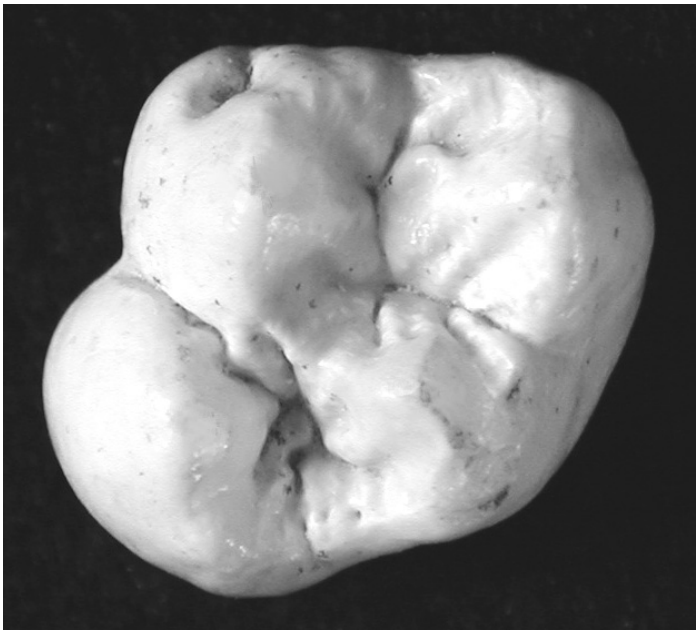
1. Neither Neandertals nor amHs exhibit hypocone reduction in M^1.
2. The frequency of Cusp 5 in Neandertals is slightly higher than the average for contemporary amHs and fossil amHs (59% vs. 56% and 50% respectively) but is within the range of all amHs as a whole[1]. Archaic *Homo sapiens* fall below the range in amHs (25%, n=4) while the single *Homo erectus* M^1 for which the trait could be reliably scored did not present a Cusp 5.

[1] In a previous study (Bailey, 2001) I found Neandertal trait frequencies for Carabelli's cusp and Cusp 5 to lie outside the range found in contemporary amHs. The discrepancy between the previous finding and these results may be attributable to 1) interobserver error, as in the previous study my observations were compared to those of a C. G. Turner; and/or 2) different sample composition (Scott and Turner, 1997).

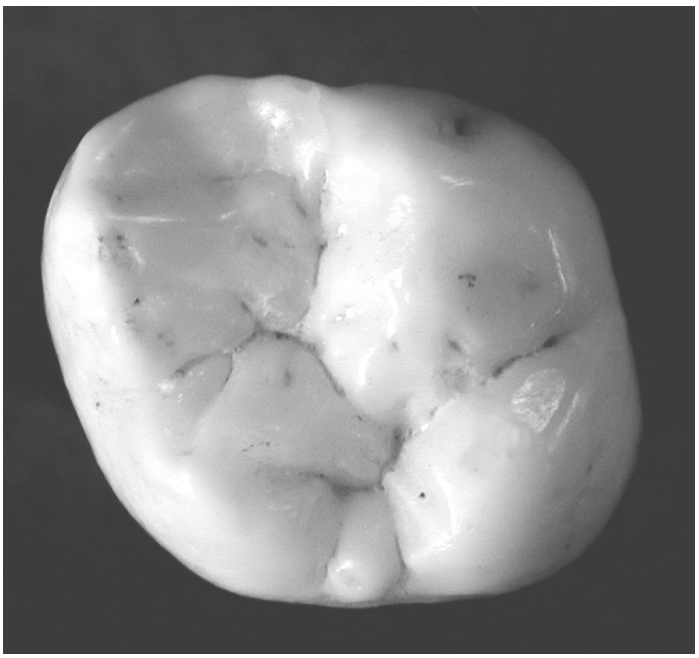
3. The frequency of Carabelli's Cusp in Neandertals is higher than the average observed in contemporary amHs (62.5% vs. 52.5%). It is also higher than that observed in both Upper Paleolithic (19%) and early amHs (43%). However, the Neandertal frequency lies within the range of contemporary amHs.
4. Mesial accessory tubercles are fairly common in all samples that could be observed (33.3%-76.9%). Because wear often precluded making an accurate observations the frequencies of this trait are based on smaller sample sizes than for many other traits. The Neandertal frequency for mesial accessory tubercles falls at the lower end of the amHs range.

M^1 summary

In terms of the key morphological traits observed in this study, Neandertal M^1s do not differ substantially from those of fossil or contemporary humans. In fact, for each trait observed, Neandertals fall within the ranges observed for contemporary amHs. Fig. 5.5 graphically illustrates this point.



a.



b.

Fig. 5.4. Neandertal maxillary molars: a) left M^1 b) right M^2

TABLE 5.3. A comparison of M^1 trait frequencies

	HYP[1]		C5		CARA		MAT	
Samples	N	%[2]	N	%	N	%	N	%
Homo erectus	2	100	1	-	*	*	*	*
Archaic *Homo sapiens*	5	100	4	25.0	4	75.0	1	-
Neandertals	**36**	**100**	**22**	**59.1**	**24**	**62.5**	**11**	**40.0**
Early amHs	7	100	4	50.0	5	40.0	1	-
Upper Paleolithic amHs	17	100	10	80.0	12	33.3	3	33.3
Contemporary amHs (pooled)	179	96.4	128	55.9	158	52.5	46	58.3
North Africa (NAF)	31	100	22	50.0	26	69.2	8	37.5
West Africa (WAF)	20	100	9	88.9	19	63.2	7	71.4
Northeast Asia (NEAS)	17	100	14	42.9	16	43.8	6	50.0
India (IND)	20	100	10	30.0	12	41.7	1	+
Near East (WAS)	5	100	5	75.0	4	50.0	1	+
Europe (EUR)	46	100	36	30.6	44	59.1	14	64.3
Australasia (AUST)	40	97.0	32	90.6	37	35.1	13	76.9

[1] Refer to Table 4.2 for trait abbreviations.
[2] A "+" indicates that a particular trait was present; a "-" indicates a particular trait was absent from the single individual scored; a * indicates no individuals could be scored for a particular trait.

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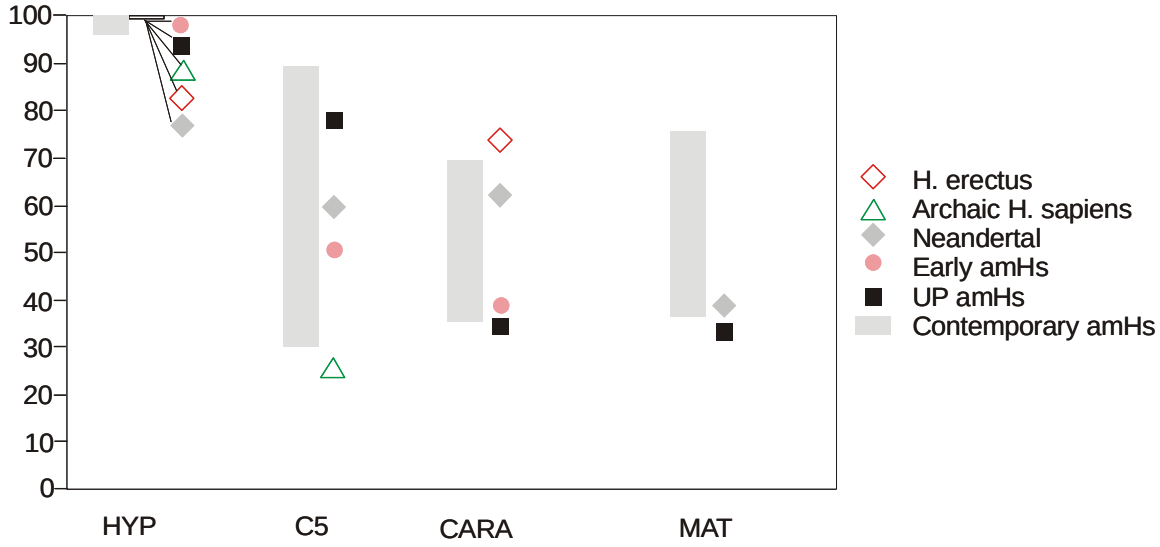


Fig. 5.5. A graphic comparison of M^1 trait frequencies among samples.

M^2 description

Neandertal M^2s are quite similar to M^1 morphologically (Fig. 5.4b). Exceptions include the higher frequency of hypocone reduction (7% vs. 0%) and a corresponding reduction in overall crown size compared to M^1. However, the frequency of traits that contribute to the tooth's overall complexity (e.g., Cusp 5 and Carabelli's cusp) change little in M^2 as compared to M^1.

M^2 comparison

Many of the traits that distinguish Neandertals from anatomically modern humans are associated with the simplification of the tooth crown in the latter group. There is a tendency in amHs for the second molar to be smaller and morphologically simpler than the first. Compared to those of contemporary amHs, Neandertal M^2s are distinctive in

their maintenance of relatively complex tooth crown morphology. A detailed comparison is presented below (see Table 5.3 and Fig. 5.6).

1. The frequency of hypocone reduction in Neandertal M^2 is much lower than the average observed in contemporary amHs (6.9% vs. 18.9%). In fact, the frequency falls outside the range of both contemporary and Upper Paleolithic amHs. Upper Paleolithic amHs, on the other hand, fall very close to the contemporary amHs mean (20% vs. 18.9%, respectively). Hypocone reduction was not observed in the early amHs, the archaic *Homo sapiens* or the *Homo erectus* samples.
2. Neandertals maintain a high frequency of Cusp 5 (68.4%), which is higher than the average observed among contemporary amHs (43.8%) but is not outside the contemporary amHs range of variation. The frequencies in early amHs (33.3%) and Upper Paleolithic amHs (38.5%) are closer to the average in contemporary amHs.
3. Relative to amHs, Neandertals are distinctive in their maintenance of a high frequency of Carabelli's cusp on M^2 (50%). This frequency falls outside the range of all amHs samples. The highest frequency of M^2 Carabelli's cusp observed among the amHs samples is 25% (early amHs). Among the contemporary amHs samples the highest frequency drops to 15% (West and North African samples). As was the case for Cusp 5, the Upper Paleolithic amHs frequency (7.1%) is very close (nearly identical) to the mean of all contemporary amHs (7.0%). Among the non-amHs groups, the Neandertal frequency for M^2 Carabelli's cusp is higher than that observed in *Homo erectus* (33.3%) but lower

than that observed in the archaic *Homo sapiens* sample (100%,). However, it should be noted that sample sizes for both these samples are very small (n=3 and n=2, respectively).

4. In all samples mesial accessory tubercles (MAT) are as likely to occur on the M^2 as on the M^1. Although the average contemporary amHs frequency of MAT is well below that of Neandertals (29.6% vs. 60%), and MAT are not found in early or in Upper Paleolithic amHs, the Neandertal frequency is within the range observed in contemporary amHs.

M^2 summary

For two of the four traits observed on the M^2, Neandertal trait frequencies fall within the ranges observed in contemporary amHs. Of the contemporary amHs they are closest to the frequencies observed in the West African sample for both Cusp 5 (68.4% vs. 72.2%) and MAC (60% vs. 66.7%). Their frequency for Carabelli's cusp is high relative to all but the archaic *Homo sapiens* group (n=2), while their frequency for hypocone reduction aligns them with other fossil hominids (Upper Paleolithic sample excluded). The Upper Paleolithic amHs sample fits well within the ranges of variation in contemporary amHs for all trait frequencies. Excepting their complete lack of hypocone reduction, the early amHs sample also fits well within the trait frequency ranges observed in contemporary amHs.

TABLE 5.4. A comparison of M^2 trait frequencies

	HYP[1]		C5		CARA		MAT	
Samples	No.	%[2]	No.	%	No.	%	No.	%
Homo erectus	4	100	4	25.0	3	33.3	3	33.3
Archaic *Homo sapiens*	4	100	3	100	2	100	1	+
Neandertals	**29**	**93.1**	**19**	**68.4**	**20**	**50.0**	**10**	**60.0**
Early amHs	5	100	3	33.3	4	25.0	1	-
Upper Paleolithic amHs	15	80.0	13	38.5	14	7.1	6	0.0
Contemporary amHs (pooled)	164	81.1	153	43.8	158	7.0	108	29.6
North Africa (NAF)	21	90.5	21	57.1	20	15.0	16	37.5
West Africa (WAF)	20	85.0	18	72.2	20	15.0	12	66.7
Northeast Asia (NEAS)	16	81.2	14	21.4	16	0.0	11	27.3
India (IND)	19	73.7	15	0.0	18	0.0	12	16.7
Near East (WAS)	5	60.0	5	20.0	5	20.0	5	40.0
Europe (EUR)	47	76.6	45	24.4	45	2.2	34	35.3
Australasia (AUST)	36	86.1	35	74.3	34	8.8	25	40.0

[1] Refer to Table 4.2 for trait abbreviations.
[2] A "+" indicates that a particular trait was present; a "-" indicates a particular trait was absent from the single individual scored.

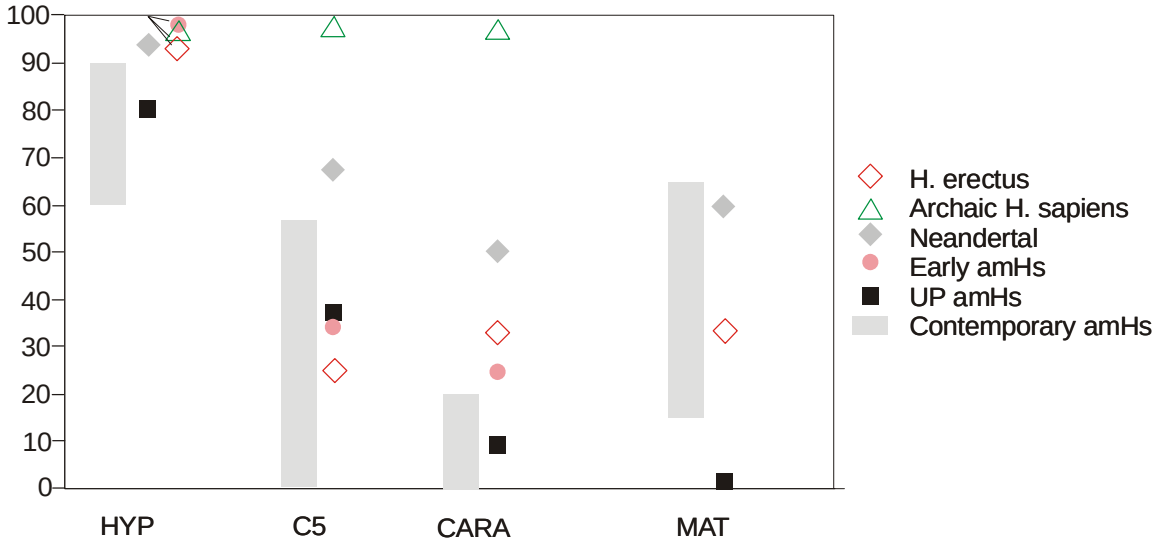


Fig. 5.6. A graphic comparison of M^2 trait frequencies among samples.

Mandibular premolars

P_3 description

The Neandertal P_3 is triangular in outline and tends to be asymmetrically shaped – often (42%) markedly so (Fig. 5.7a). It is predominantly a bicuspid tooth – having lingual and buccal main cusps – although accessory lingual cusps do occur in moderate frequencies (19.4%). Relative to the buccal cusp, the metaconid tends to be centrally (65.4%) or distally (30.8%) placed and only is only rarely (3.8%) mesially placed. A mesially placed metaconid co-occurs with the presence of a distolingual accessory cusp. The metaconid is often fairly well developed, with an independent cusp tip, although it is sometimes attached to the buccal cusp via a small crest (or *transverse* crest: 13.6%). The buccal cusp often exhibits distal (88%) and (less often) mesial (23%) accessory ridges. A

lingual marginal groove commonly occurs (73.7%) and, when it does, it is located mesially on the tooth (mesial lingual groove).

P_3 comparison

Frequencies for the dental traits on P_3 are presented in Table 5.5 and graphically depicted in Fig. 5.8. A comparison between Neandertals and other groups follows:

1. Accessory lingual cusps are more common in contemporary amHs (30.4%) and early amHs (25%) than they are in Neandertals (19.4%). Like Neandertals, Upper Paleolithic amHs present a relatively low frequency for accessory lingual cusps (11%), while the *Homo erectus* sample lacks accessory cusps altogether. One of the three archaic *Homo sapiens* individuals (33.3%) exhibits an accessory lingual cusp. Unapparent from trait frequencies is the variation in lingual cusp form and number observed in contemporary amHs. Within the contemporary amHs group individuals may present as many as four lingual cusps or may lack a lingual cusp completely. Neither of these conditions are found in any fossil sample.
2. The P_3 metaconid may be mesially (M), centrally (C) or distally (D) placed. With few exceptions the metaconid is most frequently centrally placed. In Neandertals, when the metaconid is not centrally placed it is more often placed distally (30.8%) than mesially (3.8%). This is just the opposite of what is found in most other samples, in which the pattern of frequencies is C>M>D. The average for contemporary amHs, for example, is C (55%) > M (35.7%) > D (6.4%). However, the Upper Paleolithic and North African samples show a pattern C>D=M, and the Near East and Australasian samples, show the pattern M>C>D.

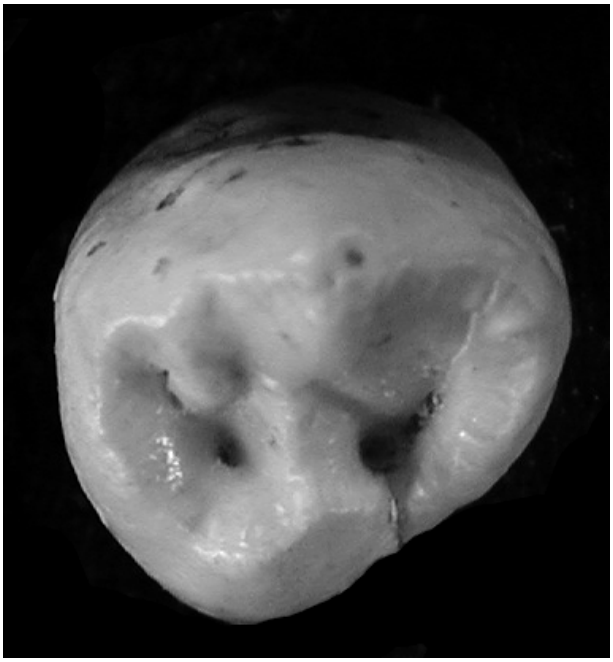
3. Both the lingual and buccal cusps of P_3 possess an essential ridge that projects toward the central groove. Quite often the two ridges fuse and form a continuous ridge or "transverse crest" that connects the protoconid and metaconid. The frequency of the transverse crest in Neandertals (79.2%) falls at the high end of the range for contemporary amHs (45%-87.5%), and is most similar to that observed for Upper Paleolithic amHs and *Homo erectus* (both 80%). Both of the individuals in the archaic *Homo sapiens* sample show this character (100%), while early amHs show a frequency (66.7%) that is closer to the average for contemporary amHs (68.1%).
4. The frequency of mesial (MAR) and distal accessory ridges (DAR) is higher, on average, in fossil hominids than in contemporary amHs. The frequency of the DAR observed in Neandertals (88.2%) lies outside the range observed in contemporary amHs (31%-68.8%), while the frequency of the MAR (23.1%) is within the range in contemporary amHs (0%-31.3%). Worth noting here is the presence, in contemporary amHs, of an accessory ridge that diverges obliquely from the top or middle of the buccal essential ridge, such that the essential ridge appears to be bifurcated. This ridge does not occur in any of the fossil hominid samples. Even more, it varies considerably within contemporary amHs and, thus, has the potential to be a useful population discriminator.
5. P_3s of both modern humans and Neandertals may have a mesial lingual groove. The high frequency of this character in Neandertals (73.7%) falls outside the

range in amHs (9.1%-56.3%). It is closer to (although higher than) that found in *Homo erectus.*

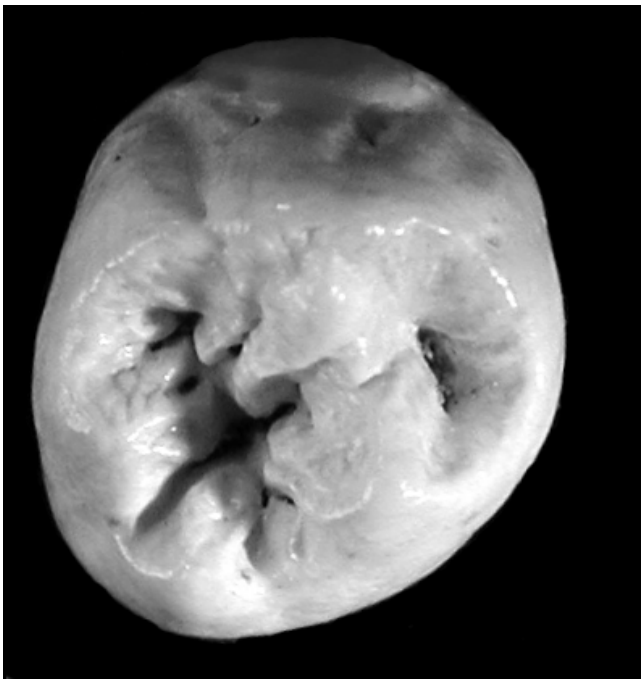
6. Finally, although Neandertals and contemporary amHs tend to have somewhat asymmetrical P_3 crowns, strong asymmetry is far more frequent in Neandertals (41.7%) than in contemporary amHs (7.5%). Strongly asymmetrical P_3 crowns are not present in the Upper Paleolithic sample. However, the frequency of strongly asymmetrical P_3 in other fossil hominids is similar to that observed in Neandertals.

P_3 summary

Relative to contemporary amHs, the Neandertal sample exhibits distinctive trait frequencies for three of the seven P_3 traits reported here (the mesial lingual groove, crown asymmetry and the distal accessory ridge). While Neandertals are not distinctive among fossil humans for mesial lingual groove and crown asymmetry, they do exhibit an unusually high frequency of the distal accessory ridge. For the traits that fall within the range of contemporary amHs, there is no consistent pattern regarding phenetic affinity. In one case Neandertals are more similar to the North African sample (P_3 lingual accessory cusp), while in another, they are more similar to the Northeast Asian sample (transverse crest). In the last case they are closer to the West African sample (mesial accessory ridge).



a.



b.

Fig. 5.7. Neandertal mandibular premolars: a) left P_3 b) left P_4

TABLE 5.5. A comparison of P_3 trait frequencies

	PLC[1]		METPOS				TRC		DAR		MAR		MLG		ASM	
Samples	N	%	N	M	C	D	N	%	N	%	N	%	N	%	N	%
Homo erectus	10	0.0	12	25.0	58.3	16.7	12	80.0	9	66.7	11	27.3	11	63.6	5	40.0
Archaic *Homo sapiens*	3	33.3	3	33.3	33.3	33.3	3	66.7	3	66.7	3	0.0	2	100	2	50.0
Neandertal	**31**	**19.4**	**26**	**3.8**	**65.4**	**30.8**	**24**	**79.2**	**17**	**88.2**	**13**	**23.1**	**19**	**73.7**	**12**	**41.7**
Early amHs	4	25.0	3	33.3	66.7	0.0	3	66.7	2	50.0	2	0.0	3	0.0	3	33.3
Upper Paleolithic amHs	9	11.1	11	27.3	45.4	27.3	10	80.0	7	71.4	8	0.0	6	50.0	3	0.0
Contemporary amHs (avg)	138	30.4	140	35.7	55.0	6.4	137	68.1	118	50.8	130	9.5	127	38.5	120	7.5
North Africa (NAF)	21	19.0	21	4.8	81.0	4.8	21	66.7	16	56.0	21	14.3	20	17.6	21	14.2
West Africa (WAF)	19	21.1	19	47.4	52.6	0.0	19	47.4	18	55.6	19	21.1	19	26.3	17	5.9
Northeast Asia (NEAS)	11	9.1	11	18.2	72.7	9.1	11	81.8	11	63.6	11	0.0	11	9.1	11	0.0
India (IND)	20	20.0	20	15.0	80.0	5.0	20	45.0	14	50.0	17	0.0	16	42.1	19	0.0
Near East (WAS)	16	50.0	16	43.8	37.5	18.8	16	87.5	14	50.0	13	0.0	16	56.3	7	14.3
Europe (EUR)	35	40.0	35	42.9	48.6	2.9	34	50.0	29	31.0	33	9.1	35	42.9	30	10.0
Australasia (AUST)	16	43.8	18	72.2	16.7	11.1	17	53.0	16	68.8	16	31.3	10	43.8	15	6.7

[1] Refer to Table 4.2 for trait abbreviations.

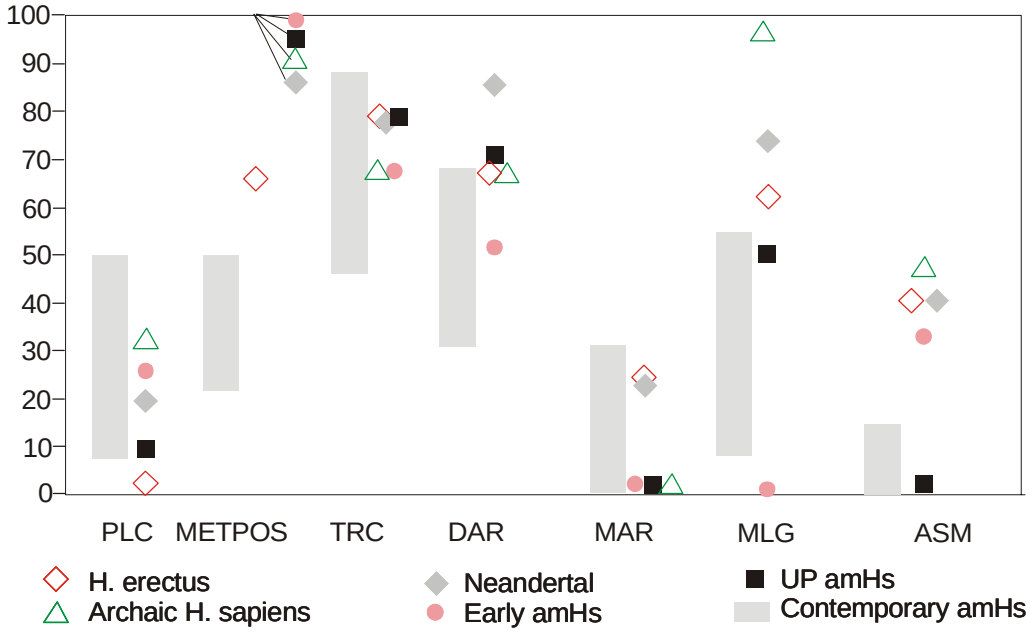


Fig. 5.8. A graphic comparison of P_3 trait frequencies among samples.

Overall, P_3 morphology does not appear to have particularly strong discriminatory power for sorting Neandertals from amHs. Neandertal P_3s do tend to exhibit greater occlusal complexity, but this is true of other fossil hominids as well. Certain morphology, however, does appear to be unique to contemporary amHs and is likely derived for that group. In particular, multiple (>2) lingual cusps, the lack of a well-defined P_3 metaconid, and the bifurcated buccal essential ridge may be derived in contemporary amHs. Because these characters also vary geographically, they may be good discriminators among contemporary amHs populations.

P_4 description

The Neandertal P_4 is characterized by a complex occlusal topography and an asymmetrical lingual contour (Fig 5.7b). The tooth's occlusal complexity results from a combination of a strong and continuous transverse crest (connecting the buccal and lingual cusps), a high and well-developed metaconid, and extra fissures, ridges and lingual tubercles. Unlike the case in the P_3, the frequency of multiple lingual cusps in P_4s is high in Neandertals. In 48% of the cases two lingual cusps are present and in 45% of the cases there are three. The remaining 11% present no lingual accessory cusps. In contrast to the P_3, the metaconid of P_4 is almost always (96%) mesially placed and is never distally placed. Although the metaconid is mesially placed, the mesiolingual lobe is often smaller than that of the distolingual lobe. This disparity gives the tooth its characteristic asymmetrical shape, which is present in 90% of the sample.

P_4 comparison

In general, the contemporary amHs P_4 contrasts with the typical Neandertal P_4 in its greatly simplified occlusal morphology. Frequencies for the dental traits on P_4 are presented in Table 5.6 and graphically depicted in Fig. 5.9. A comparison between Neandertals and other groups follows:

1. Both Neandertals and modern humans often exhibit more than one lingual cusp, although the Neandertal trait frequency (88.9%) falls just outside the range observed in contemporary amHs (20%-87.5%). *Homo erectus*, early amHs and Upper Paleolithic amHs samples are more similar to the contemporary amHs

sample in their trait frequencies, while the archaic *Homo sapiens* sample (n = 2, 100%) is even higher than the Neandertal sample.

2. A mesially placed metaconid is typical of Neandertals but is also common in other fossil and contemporary humans. The Neandertal frequency (96.0%) is higher than that observed in any amHs (20%-54.5%), but it is close to that found in *Homo erectus* (90%) and is exceeded by the archaic *Homo sapiens* sample (n = 3, 100%).
3. A transverse crest that forms an enamel bridge connecting the buccal and lingual cusps is typical of Neandertal P_4s (87.5%) but much less common in contemporary (0%-6%) and Upper Paleolithic amHs (18%) samples. The crest is more frequent in fossil hominids than in contemporary amHs (41.7% in *Homo erectus*, 66.7% in archaic *Homo sapiens* and 50% in early amHs). However, these frequencies are well below that observed in Neandertals. Not apparent from mere trait frequencies is the fact that in Neandertals, the transverse crest is usually well-developed and mesially placed, while in both fossil and contemporary amHs the transverse crest is more weakly developed and centrally placed when present.
4. The typical Neandertal P_4 presents an asymmetrical lingual contour (90%), while the modern human P_4 is almost invariably symmetrical (asymmetry was noted in only 0%-6% of the populations sampled). Archaic *Homo sapiens* and *Homo erectus* samples show asymmetry frequencies that are higher than in amHs; however, they are still low compared to Neandertals (36.4% and 33.3% respectively).

5. Mesial and distal accessory ridges are often present in both fossil and recent humans. The frequency of the mesial accessory ridge in Neandertals (16.7%) is within the range observed in amHs (5.9%-50%), and similar to the frequency found in *Homo erectus* (14.3%). The frequency of the distal accessory ridge found in Neandertals (91.7%) falls outside the range of amHs variation (12.5%-50%) and is similar to frequencies found in both archaic *Homo sapiens* (100%) and *Homo erectus* (85.7%).
6. The mesial lingual groove is, on average, more frequent in contemporary amHs (0%-56%, average 27%) than in Neandertals (12%). Neandertals and other fossil hominids are similar with respect to their low frequencies of this trait.

P^4 summary

For five of the seven morphological traits scored on the P_4 Neandertals fall outside the range of contemporary amHs (Fig 5.9). Two of these trait frequencies (asymmetry and transverse crest) are distinctive with respect to other fossil hominids as well. The other three trait frequencies (multiple lingual cusps, metaconid placement and distal accessory ridge) are similar to those observed in *Homo erectus* and/or archaic *Homo sapiens*. In all cases the Upper Paleolithic and early amHs samples fall closer to the contemporary amHs than to the Neandertal sample for P_4 trait frequencies. In one case (multiple lingual cusps) the trait frequency observed in the *Homo erectus* sample is more similar to that of the amHs samples than it is to that of the Neandertal sample; and in two cases (asymmetry and transverse crest) the *Homo erectus* frequencies are intermediate between contemporary amHs and Neandertals frequencies.

TABLE 5.6. A comparison of P_4 trait frequencies

	PLC[1]		METPOS			TRC		DAR		MAR		MLG		ASM	
Samples	N	%[2]	N	M	C	N	%	N	%	N	%	N	%	N	%
Homo erectus	9	66.7	10	90.0	10.0	12	41.7	7	85.7	7	14.3	7	14.3	11	36.4
Archaic *Homo sapiens*	2	100	3	100	0.0	3	66.7	2	100	3	33.3	3	0.0	3	33.3
Neandertals	**27**	**88.9**	**26**	**96.0**	**7.4**	**24**	**87.5**	**12**	**91.7**	**12**	**16.7**	**17**	**11.8**	**20**	**90.0**
Early amHs	3	66.7	2	50.0	50.0	2	50.0	2	50.0	2	50.0	2	0.0	4	0.0
Upper Paleolithic	9	44.4	9	45.5	54.5	11	18.2	3	33.3	3	0.0	4	0.0	6	0.0
Contemporary amHs (pooled)	131	56.6	132	70.5	27.3	125	2.3	106	36.8	112	21.4	102	26.5	125	5.9
North Africa (NAF)	17	58.8	18	72.2	27.8	16	6.3	15	26.7	16	6.3	16	56.3	17	0.0
West Africa (WAF)	19	63.2	19	78.9	21.1	19	5.3	16	50.0	18	38.9	*	*	18	5.6
Northeast Asia (NEAS)	10	50.0	10	60.0	40.0	10	0.0	8	12.5	9	22.2	8	37.5	8	0.0
India (IND)	20	20.0	20	60.0	40.0	17	0.0	14	14.3	17	5.9	20	15.0	18	6.0
Near East (WAS)	15	40.0	15	80.0	20.0	15	0.0	9	66.7	9	22.2	15	0.0	6	0.0
Europe (EUR)	34	55.9	34	67.6	32.4	30	0.0	31	32.3	30	23.3	33	36.4	40	0.0
Australasia (AUST)	16	87.5	16	75.0	25.0	18	5.6	13	61.5	13	30.8	10	0.0	18	6.0

[1] Refer to Table 4.2 for trait abbreviations.
[2] A * indicates no individuals could be scored for a particular trait.

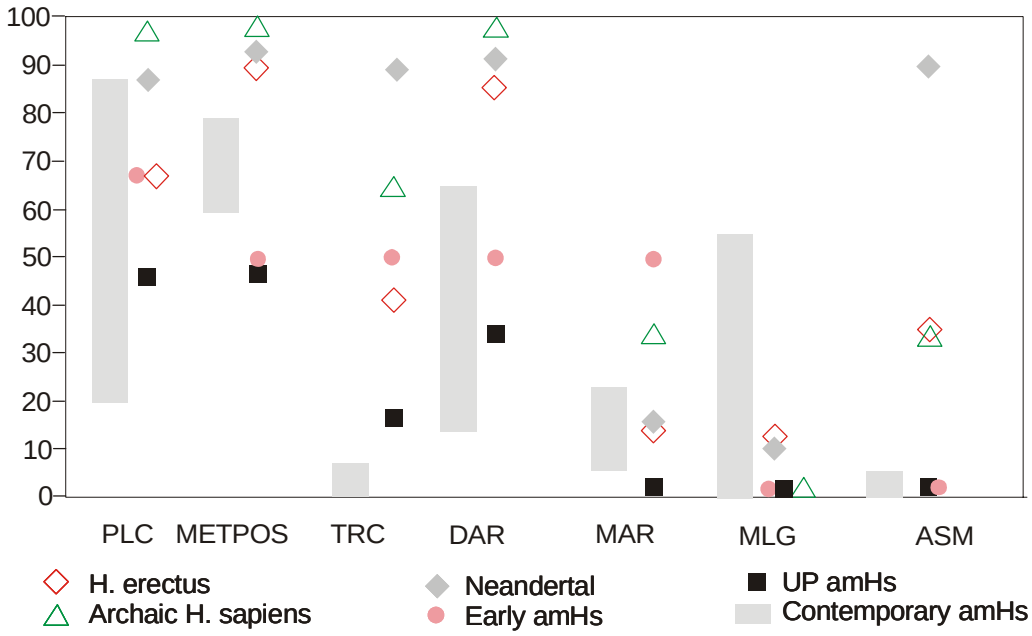


Fig. 5.9. A graphic comparison of P_4 trait frequencies among samples.

Where Neandertals fall within (or just outside) the range of contemporary amHs variation, there is no consistency regarding to which contemporary amHs group they are closest phenetically. For multiple lingual cusps, Neandertals are closest to the Australasian sample (88%); for MAR they are closest to West African sample; and, for MLG they are closest to the Indian sample.

Overall, Neandertal P_4s seem to be quite distinctive in their occlusal morphology. While each of the traits that contribute to the uniqueness of the Neandertal P_4 can be found in individuals within the modern human populations, the combination of these characters (asymmetrical crown contour, large, mesially placed metaconid and a strong, continuous transverse crest) is not observed in any amHs sample. In fact, only 2.4% of

the contemporary amHs exhibited even two of the traits in combination. In marked contrast, 35% of Neandertals exhibited two traits and 59% exhibited all three traits in combination. Finally, although not apparent from the trait frequencies presented here, one of the most notable features of the modern human P_4s is that the metaconid may be so reduced that it forms only a lingual shelf or is lacking altogether. This condition was never observed in the Neandertal sample.

Mandibular molars

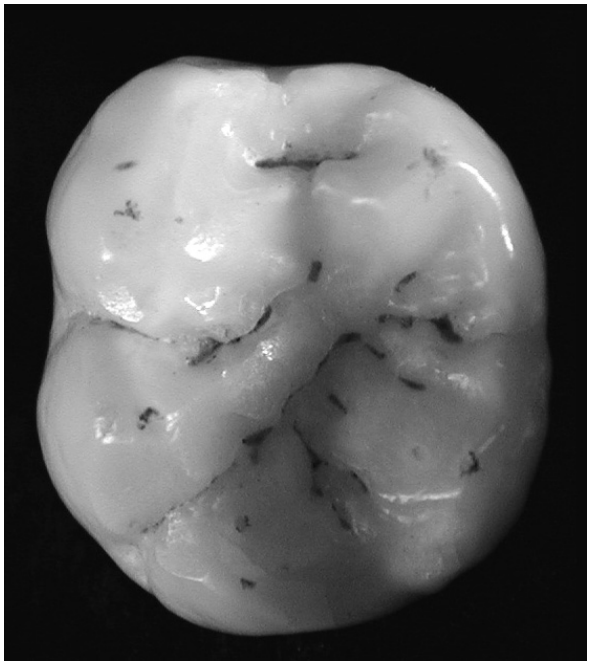
M_1 description

The Neandertal M_1 tends to be occlusally complex, possessing extra fissures and crests (Fig. 5.10a). This tooth always possesses at least five cusps and nearly always presents a Y-pattern (97%). In 28% of the specimens cusp 6 (C6) was also observed and 19% exhibited Cusp 7 (C7). The protostylid (2%) and distal trigonid crest (3.6%) are rare and the deflecting wrinkle was not observed. The most remarkable features observed on this tooth are a wide and deep anterior fovea bordered distally by a continuous mid-trigonid crest. A well-developed anterior fovea occurs in 87.1% of the Neandertal M_1s sampled and a well-developed and continuous mid-trigonid crest occurs in 96%. Not uncommonly, a very low mesial marginal ridge (one that was at the level of, or lower than, the occlusal basin) was observed to co-occur with these features. However, data on its frequency were not systematically collected.

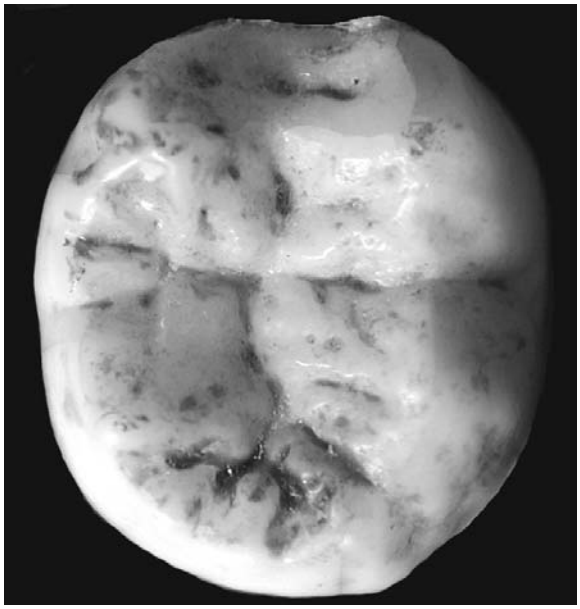
M_1 comparison

Frequencies for dental traits on M_1 are presented in Table 5.7 and graphically depicted in Fig. 5.11. A trait-by-trait comparison follows:

1. Neandertals, like all groups sampled, exhibit high frequencies of the Y-pattern in M_1. The frequency is only slightly higher in fossil hominids (97.1-100%) than in contemporary amHs (87.5%-100%).
2. Neither Neandertals nor other fossil hominids possess four cusped M_1s. In contrast, Upper Paleolithic amHs and contemporary amHs exhibit low-to-moderate frequencies of four-cusped M_1 (0%-20%).
3. The Neandertal frequency for C6 on M_1 (27.8%) is within the range observed in amHs (0%-44.4%) and is close to that observed in *Homo erectus* (28.6%).
4. The Neandertal frequency for C7 (18.8%) is also within the range observed in contemporary amHs (3.3%-61.1%); and is somewhat lower than that observed in other fossil hominids (25%-45%).
5. The Neandertal sample exhibits high frequencies of the mid-trigonid crest (96.0%). This frequency is well outside the range observed in amHs groups (0%-14.3%). The *Homo erectus* sample has a similarly low frequency (11%) while the archaic *Homo sapiens* sample (75%) is more similar to the Neandertal sample
6. Like the mid-trigonid crest, the Neandertal frequency for anterior fovea (87.1%) is outside the range of contemporary amHs (11.1%-37.5%). However, other fossil hominids (early amHs excepted) also exhibit high frequencies of the anterior fovea.



a.



b.

Fig. 5.10. Neandertal mandibular molars: a) left M_1 b) right M_2

TABLE 5.7. A comparison of M_1 trait frequencies

	YPAT[1]		4CSP		DW		DTC		MTC		C6		C7		AFOV	
Samples	N	%[2]	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Homo erectus	10	100	12	0.0	6	66.7	8	0.0	9	11.1	7	28.6	10	40.0	7	71.4
Archaic *Homo sapiens*	5	100	6	0.0	2	0.0	3	0.0	4	75.0	1	-	5	20.0	4	100
Neandertal	**33**	**97.0**	**44**	**0.0**	**21**	**0.0**	**28**	**3.6**	**25**	**96.0**	**18**	**27.8**	**31**	**19.4**	**31**	**87.1**
Early amHs	4	100	4	0.0	2	50.0	3	0.0	3	0.0	4	0.0	4	25.0	3	33.3
Upper Paleolithic amHs	19	100	25	4.0	11	18.2	16	0.0	14	0.0	13	23.1	20	5.0	13	76.9
Contemporary amHs (pooled)	139	95.0	145	5.4	57	22.8	124	0.8	118	0.8	119	17.6	148	13.5	98	24.5
North Africa (NAF)	30	93.3	30	3.3	9	33.3	27	0.0	22	0.0	27	7.4	30	10.0	21	14.3
West Africa (WAF)	17	100	18	0.0	7	28.6	18	0.0	18	0.0	16	18.8	18	61.1	18	27.8
Northeast Asia (NEAS)	11	90.9	11	0.0	7	14.3	9	11.1	10	0.0	9	44.4	11	9.1	9	33.3
India (IND)	18	100	10	20.0	4	50.0	16	0.0	14	0.0	11	0.0	18	5.6	9	11.1
Near East (WAS)	8	87.5	12	0.0	5	20.0	7	0.0	7	14.3	11	9.1	12	8.3	8	37.5
Europe (EUR)	29	96.6	32	9.4	12	8.3	22	0.0	21	0.0	24	8.3	30	3.3	16	25.0
Australasia (AUST)	26	92.3	32	3.1	13	15.4	25	0.0	26	0.0	21	42.9	29	10.3	17	29.4

[1] Refer to Table 4.2 for trait abbreviations.
[2] A "-" indicates a particular trait was absent from the single individual scored.

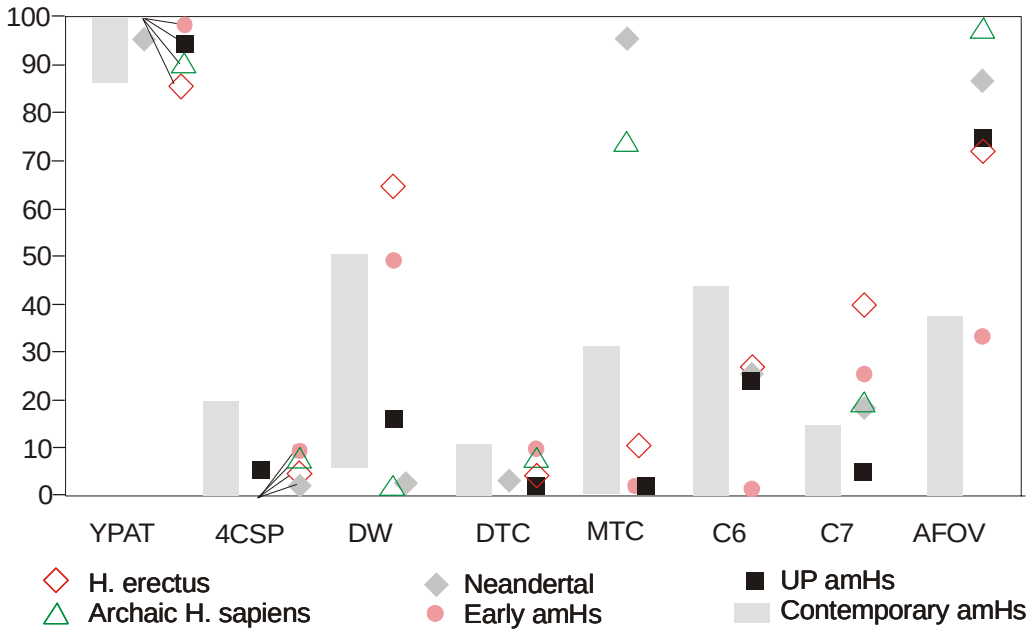


Fig. 5.11. A graphic comparison of M_1 trait frequencies among samples..

M_1 summary

The Neandertal M_1 is, overall, quite similar to the M_1 of contemporary amHs. Where they differ they often are aligned with other fossil hominids groups. The most notable exception is the Neandertals' unusually high frequency of the mid-trigonid crest. Where Neandertal M_1 trait frequencies fall within the range of contemporary amHs there is no clear pattern with regard to which of the contemporary amHs groups they are most similar to phenetically.

M_2 description

The Neandertal M_2 is very similar to the M_1 in its morphology (Fig 5.10). None of the M_2s possess fewer than five cusps and 78.8% maintain the Y-pattern. Cusp 6 occurs more frequently on M_2 than on M_1 (50% and 28% respectively). As is the case for

M_1, the protostylid (2%) and distal trigonid crest (8%) are rare and the deflecting wrinkle was not observed. As with M_1, the anterior fovea and mid-trigonid crest occur in high frequencies on M_2 (87% and 95.7% respectively). This is particularly significant because the mid-trigonid crest in amHs it is found almost exclusively on the M_1.

M_2 comparison

Frequencies for the dental traits on M_2 are presented in Table 5.8 and graphically depicted in Fig. 5.12. A comparison between Neandertals and other groups follows:

1. Neandertals, like other fossil hominids, maintain a relatively high frequency of Y-pattern in M_2 (78.8%). In contrast, the frequency of Y-pattern in M_2 drops substantially in contemporary amHs (9.1%-40%) and Upper Paleolithic amHs (52.4%) samples.
2. Neandertals rarely exhibit four-cusped M_2s: only one in 37 (2.7%) lacked a hypoconulid. In contrast, Upper Paleolithic amHs and contemporary amHs exhibit considerably high frequencies of four-cusped M_2 (20.7%-100%).
3. Neandertal M_2s show relatively high frequencies of C6 (52.6%). This frequency falls outside the range observed in both fossil and contemporary humans.
4. Neandertals exhibit C7 on M_2 in moderate frequency (14.8%). This is outside the range observed in contemporary amHs (0%-11.1%), substantially higher than that observed in Upper Paleolithic amHs and lower than that observed in early amHs (33.3%). It is also lower than that observed in archaic *Homo sapiens* and *Homo erectus* (33.3% and 36.4%, respectively).

5. As was the case for M_1, Neandertals exhibit exceptionally high frequencies of the mid-trigonid crest on M_2 (95.8%). This is well outside the range observed in all amHs groups (0%-10%). The next highest frequency (75%) occurs in archaic *Homo sapiens*.
6. The Neandertal M_2 is also distinctive in its maintenance of a high frequency of anterior fovea (87.5%). This frequency is even higher than that observed in *Homo erectus* and archaic *Homo sapiens* samples (both 75%), and well above that in both fossil and contemporary amHs groups (23.8% -62.1%) .

M_2 summary

The Neandertal frequencies for six of the eight traits observed on the M_2 fall outside the range observed in contemporary amHs. The high frequencies of Y-pattern and Cusp 6, together with the low frequency of 4-cusped M_2 and relatively higher frequency of distal trigonid crest, align Neandertals with other fossil hominids. As was the case for M_1, Neandertals are unique among all groups in their high frequency of expression of the mid-trigonid crest and anterior fovea.

TABLE 5.8. A comparison of M_2 trait frequencies

	YPAT[1]		4CSP		DW		DTC		MTC		C6		C7		AFOV	
Samples	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Homo erectus	11	90.9	15	0.0	9	22.2	12	8.3	13	7.7	5	40.0	11	36.4	12	75.0
Archaic *Homo sapiens*	6	66.7	6	0.0	3	0.0	4	0.0	4	75.0	4	0.0	6	33.3	4	75.0
Neandertal	**34**	**79.4**	**37**	**2.7**	**20**	**0.0**	**27**	**11.1**	**24**	**95.8**	**19**	**52.6**	**28**	**14.8**	**24**	**87.5**
Early amHs	2	100	3	0.0	2	0.0	2	0.0	2	0.0	2	0.0	3	33.3	2	50.0
Upper Paleolithic amHs	21	52.4	18	27.8	14	14.3	20	0.0	17	0.0	15	20.0	18	0.0	17	47.1
Contemporary amHs (pooled)	147	25.2	130	57.7	119	1.7	147	0.0	148	4.1	124	13.7	149	3.4	139	43.2
North Africa (NAF)	22	13.6	22	54.5	20	0.0	22	0.0	22	4.5	21	0.0	22	4.5	21	23.8
West Africa (WAF)	23	30.4	17	17.6	14	7.1	18	0.0	18	0.0	15	33.3	18	11.1	18	27.8
Northeast Asia (NEAS)	13	7.7	12	33.3	10	0.0	13	0.0	13	0.0	10	30	13	0.0	11	54.5
India (IND)	20	40.0	16	100	16	0.0	20	0.0	20	0.0	16	0.0	20	0.0	19	26.3
Near East (WAS)	11	9.1	10	80.0	8	0.0	10	0.0	10	10.0	10	20.0	11	0.0	9	44.4
Europe (EUR)	32	28.1	32	81.3	28	0.0	34	0.0	34	0.0	31	3.2	34	0.0	32	53.1
Australasia (AUST)	31	25.8	29	20.7	23	4.3	30	0.0	31	6.5	21	28.6	31	3.2	29	62.1

[1] Refer to Table 4.2 for trait abbreviations.

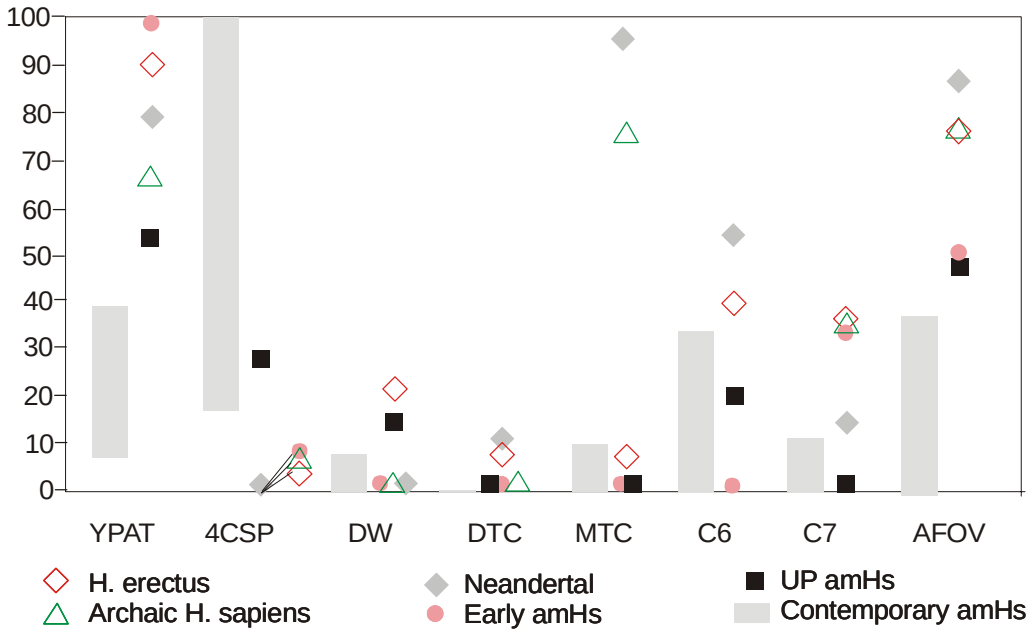


Fig. 5.12. A graphic comparison of M_2 trait frequencies among samples.

The Neandertal dental pattern: Summary of the morphology

The Neandertal dental morphological pattern can be summarized in terms of high and low frequency traits (Table 5.9). Although anterior tooth traits were not the subject of this work, they have been analyzed previously (Bailey, 2000a; Coppa et al., 2001) and are presented here to provide a more comprehensive assessment of the Neandertal dental pattern. The traits followed by an asterisk (*) are new traits that have resulted from the preceding analysis.

Many of the trait frequencies that make up the Neandertal dental pattern are within the range of contemporary amHs groups. However, the overall pattern of high and low frequency traits does not correspond to any observed in contemporary amHs. Moreover, there are several traits for which the Neandertal frequencies appear to be unique among both fossil and recent humans. These include the transverse crest and asymmetry of P_4 and the mid-trigonid crest on M_1 and M_2. Well-developed crests on the

protoconid and metaconid of P_4 are more prevalent in Neandertals than contemporary amHs, but what makes them distinctive when compared to all fossil and recent humans is the presence of an enamel bridge that connects these cusps and transects the interlobal groove. The asymmetry of P_4 observed in Neandertals can be quite remarkable and is rarely observed in fossil or contemporary amHs. Moreover, *Homo erectus* tends to have the same configuration as amHs, rather than that observed in Neandertals. Finally, although the essential crests of the lower molar protoconid and metaconid may be well developed in amHs and *Homo erectus*, they generally do not join to form a continuous ridge as they do in Neandertals and some archaic *Homo sapiens*. Instead, the cusps are separated by the sagittal sulcus, which either terminates in the anterior fovea or runs the length of the tooth; and most often the crests are not very well developed at all.

TABLE 5.9. The Neandertal dental pattern: high and low frequency traits

High Frequency Traits	Low Frequency Traits
Incisor shoveling	Incisor double shoveling
Incisor labial convexity	Four-cusped M_2
Incisor lingual tubercles	Three-cusped M^2
Canine mesial ridge	Deflecting Wrinkle*
Cusp 5 – M^1, M^2	Distal Trigonid Crest*
Carabelli's cusp – M^1, M^2	Mesial lingual groove – P_4*
Mesial lingual groove – P_3*	
Transverse crest – P_3, P_4*	
Asymmetry – P_3, P_4*	
Multiple lingual cusps – P_4*	
Mesially placed metaconid – P_4*	
Distal accessory ridge – P_3, P_4*	
Cusp 6 – M_2*	
Mid-Trigonid Crest – M_1, M_2 *	
Large anterior fovea – M_1, M_2 *	
Y-groove pattern – M_2	

Dental morphometrics

The metric portion of this dissertation is limited to the molars and to P_4. The morphometric analysis of molars (both mandibular and maxillary) consists of measurements of relative cusp areas, cusp angles and relative occlusal polygon area. Originally I planned to focus only on the molars but the asymmetry noted in P_4 prompted undertaking a metric analysis of its crown contour as well.

Mandibular molars

Relative cusp areas

A statistical summary of the relative size of the main cusps for each of the groups is provided in Tables 5.10 and 5.11. Excepting the *Homo erectus* and early amHs samples, the protoconid comprises the largest proportion of the total crown area of both M_1 and M_2. The pattern of M_1 relative cusp areas is PROPCT>METPCT>HYPCT≥ ENTPCT >HYPDPCT[2] in archaic *Homo sapiens* and Upper Paleolithic samples and PROPCT >METPCT>ENTPCT>HYPCT>HYPDPCT in Neandertal and contemporary amHs samples, while in M_2 it is PROPCT>HYPCT>METPCT≥ENTPCT>HYPDPCT in these four samples. In contrast, in both the *Homo erectus* and early amHs samples the metaconid comprises the largest proportion of the total crown area of M_1 and M_2. The corresponding patterns in relative cusp areas in these samples are: METPCT>PROPCT >HYPCT>ENTPCT>HYPDPCT for M_1 and METPCT>PROPCT>HYPPCT ><ENTPCT>HYPCT for M_2. In all samples, the protoconid comprises a slightly larger

[2] PROPCT, protoconid percent of total crown area; METPCT, Metaconid percent of total crown area; HYPCT , hypoconid percent of total crown area; ENTPCT, Entoconid percent of total crown area; HYPDPCT, hypoconulid percent of total crown area.

proportion of the total crown area of M_2 than it does in M_1 – a trend also seen in australopithecines and east African early *Homo* (Wood et al., 1983).

Inspection of the coefficients of variation (CV) shows that the protoconid is the least variable of the five cusps in all but the Upper Paleolithic sample. This is followed by the metaconid in Neandertals and contemporary amHs, whereas in *Homo erectus* the entoconid and metaconid are equally variable. In the Upper Paleolithic sample, the degree of variability in the protoconid and metaconid is reversed. Of the five cusp areas the hypoconulid (distalmost cusp) is the most variable in all samples. The protoconid and metaconid represent the mesial portion of the tooth, indicating that, in general, there is greater variation in the talonid (i.e., distally) than the trigonid (i.e., mesially).

The pattern of CVs is slightly different in the M_2. In this case, the protoconid remains the least variable of the five cusps but the variability of the metaconid and entoconid differs among the samples. *Homo erectus* and Neandertals are most similar, sharing the pattern HYPDPCT>HYPCT≥METPCT>ENTPCT>PROPCT. In contemporary amHs the pattern in M_2 and M_1 are the same, while the pattern in the Upper Paleolithic sample is different from all other samples. Considering the small sample size in the Upper Paleolithic sample, this difference may be due to sampling error.

Multiple Mann-Whitney-U tests were used to examine the significance of the differences in relative cusp areas among groups. The results are presented in Tables 5.12 and 5.13. The significance tests do not include early amHs or archaic *Homo sapiens* because each had a sample size of only two individuals. Because multiple comparisons were made, the Bonferroni Correction was used to protect against Type 1 errors and

maintain a table-wide alpha level of .05. However, some researchers feel that the Bonferroni Correction is an inappropriate method for this kind of data (e.g., Lockwood, pers. comm.) or that the costs (increase in Type II error, for example) do not outweigh the benefits (e.g., Perneger, 1998). Therefore, I have also indicated in Tables 5.12 and 5.13 where values are significant at uncorrected .05 and .01 levels.

Of all the pairwise comparisons, only one was significant according to the Bonferroni corrected significance level (0.008). The significant difference is found between *Homo erectus* and recent amHs for relative M_1 entoconid size. Even when the significant differences are taken at face value (uncorrected), there is little pattern to the distribution of significance in M_1. The relatively large protoconid observed in the M_1 of the Upper Paleolithic amHs sample may be attributable to sampling error due to its small sample size. The comparative data for M_2 indicate that the *Homo erectus* sample shows a pattern of relative cusp size that is most divergent from that seen in other groups.

TABLE 5.10. Relative cusp areas M_1 in fossil and contemporary humans

	PROPCT[2]					METPCT					HYPCT				
	X	N	S.D.	Range	CV	X	N	S.D.	range	CV	X	N	S.D.	Range	CV
HE	24.8	6	1.8	23.0-28.3	7.3	26.3	6	3.1	22.0-30.5	11.8	20.9	6	2.5	16.5-23.4	12.0
EHS	23.6	2	---	23.2-23.9	---	28.0	2	---	25.8-30.3	---	18.0	2	---	15.2-20.8	*
AHS	25.2	2	---	24.0-26.4	---	23.1	2	---	21.8-24.4	---	18.6	2	---	16.6-20.5	*
NEA	**24.2**	**12**	**2.2**	**20.4-27.8**	**9.1**	**23.6**	**12**	**3.2**	**20.2-26.3**	**13.6**	**19.3**	**12**	**3.9**	**14.5-30.8**	**20.2**
UP	26.3	4	2.7	23.5-29.5	10.3	22.1	4	1.2	20.4-23.0	5.4	22.0	4	3.4	18.3-26.4	15.5
CONT	24.9	63	2.1	20.3-30.5	8.4	22.3	63	1.9	17.5-28.4	8.5	20.1	63	2.4	16.1-29.1	11.9

	ENTPCT					HYPDPCT[1]				
	X	N	S.D.	range	CV	X	N	S.D.	range	CV
HE	15.4	6	1.8	12.6-18.2	11.7	12.7	6	2.8	10.2-17.9	22.0
EHS	16.9	2	---	16.9-17.0	---	12.4	2	---	12.3-12.5	---
AHS	18.6	2	---	16.8-20.5	---	14.8	2	---	13.4-16.2	---
NEA	**20.8**	**12**	**3.8**	**16.0-30.1**	**18.3**	**12.1**	**12**	**3.1**	**4.2-15.9**	**25.6**
UP	20.3	4	2.6	17.6-23.9	12.8	9.3	3	6.6	10.4-15.8	71.0
CONT	20.6	63	2.0	17.3-27.7	9.7	12.1	61	3.8	3.0-19.2	31.4

[1] Only molars with hypoconulid present are included in this summary. One UP M_1 and three CONT M1 lacked a hypoconulid.
[2] PROPCT, protoconid percent of total crown area; METPCT, Metaconid percent of total crown area; HYPCT , hypoconid percent of total crown area; ENTPCT, Entoconid percent of total crown area; HYPDPCT, hypoconulid percent of total crown area.

TABLE 5.11. Relative cusp areas M_2 in fossil and contemporary humans

	PROPCT[2]					METPCT					HYPCT				
	X	N	S.D.	Range	CV	X	N	S.D.	Range	CV	X	N	S.D.	Range	CV
HE	24.9	4	1.5	22.9-26.3	6.0	25.6	4	2.4	22.5-28.2	9.4	18.7	4	3.0	14.7-21.6	16.0
EHS	24.3	2	*	23.1-25.5	*	27.5	2	*	26.5-28.6	*	19.2	2	*	14.7-23.8	*
AHS	25.4	2	*	24.2-26.6	*	20.5	2	*	19.5-21.5	*	25.2	2	*	22.7-27.6	*
NEA	**26.1**	**14**	**2.9**	**18.6-29.5**	**11.1**	**21.3**	**14**	**3.8**	**16.4-30.4**	**17.8**	**23.2**	**14**	**4.1**	**16.0-31.6**	**17.7**
UP	29.8	7	2.1	28.1-33.9	7.1	21.4	7	3.5	17.8-26.7	16.4	26.3	7	3.0	21.4-30.2	11.4
CONT	26.5	88	2.8	18.8-32.3	10.6	22.8	88	3.1	15.7-32.4	13.6	24.7	88	4.2	15.1-32.4	17.0

	ENTPCT					HYPDPCT[1]				
	X	N	S.D.	Range	CV	X	N	S.D.	Range	CV
HE	15.9	4	1.2	14.4-17.2	7.5	14.8	4	3.3	10.8-19.0	22.3
EHS	21.1	2	*	20.9-21.4	*	8.0	2	*	0-16.0	*
AHS	17.9	2	*	16.9-19.0	*	11.0	2	*	7.4-14.6	*
NEA	**20.3**	**14**	**2.8**	**16.9-24.2**	**13.8**	**10.1**	**12**	**4.4**	**4.3-14.3**	**33.7**
UP	21.5	7	3.2	17.1-24.8	14.9	7.1	1	*	*	*
CONT	22.2	88	3.7	11.1-32.4	16.7	10.4	33	3.7	3.3-16.6	36.1

[1] Only molars with hypoconulid present are included in this summary. One UP M_1 and three CONT M1 lacked a hypoconulid.

[2] See Table 5.10 for abbreviations.

TABLE 5.12. Between group comparisons of relative cusp areas of M_1: (significance values based on Mann Whitney U non-parametric tests[1])

	PROPCT[2]				METPCT			
	HE	NEA	UP	REC	HE	NEA	UP	REC
M_1								
HE	----				----			
NEA	N.S.	----			N.S.	----		
UP	N.S.	N.S.	----		N.S.	N.S.	----	
REC	N.S.	N.S.	N.S.	----	**	*	N.S.	----

	HYPCT				ENTPCT			
	HE	NEA	UP	REC	HE	NEA	UP	REC
M_1								
HE	----				----			
NEA	N.S.	----			**	----		
UP	N.S.	N.S.	----		*	N.S.	----	
REC	N.S.	N.S.	N.S.	----	***	N.S.	N.S.	----

	HYPDPCT			
	HE	NEA	UP	REC
M_1				
HE	----			
NEA	N.S.	----		
UP	N.S.	N.S.	----	
REC	N.S.	N.S.	N.S.	---

[1] * Significant at .05 (uncorrected), ** significant at .01 (uncorrected). *** significant at corrected Bonferroni level (.008)

[2] See Table 5.10 for abbreviations.

TABLE 5.13. *Between group comparisons of relative cusp areas of M_2: (significance values based on Mann Whitney U non-parametric tests[1])*

	PROPCT[2]				METPCT			
	HE	NEA	UP	REC	HE	NEA	UP	REC
M_2								
HE	----				----			
NEA	N.S.	----			*	----		
UP	**	**	----		N.S.	N.S.	----	
REC	N.S.	N.S.	**	----	N.S.	N.S.	N.S.	----

	HYPCT				ENTPCT			
	HE	NEA	UP	REC	HE	NEA	UP	REC
M_2								
HE	----				----			
NEA	*	----			**	----		
UP	*	N.S.	----		*	N.S.	----	
REC	**	N.S.	N.S.	----	**	N.S.	N.S.	----

	HYPDPCT			
	HE	NEA	UP	REC
M_2				
HE	----			
NEA	*	----		
UP	**	**	----	
REC	**	**	N.S.	---

[1] * Significant at .05 (uncorrected), ** significant at .01 (uncorrected). *** significant at corrected Bonferroni level (.008)

[2] See Table 5.10 for abbreviations.

Results of a Principal Component Analysis (PCA) for absolute and relative cusp areas of M_1 and M_2 are presented in Table 5.14. In the PCA of absolute cusp areas for M_1, the first principal component (PCI) accounts for approximately 55% of the total variance, for M_2 PCI accounts for approximately 48% of the total variance. In both cases the eigenvectors have the same sign, and approximately equal weight is given to each of the cusps. This suggests that the major separating effect is size.

When size is controlled for and a PCA is undertaken using relative cusp areas, PCI accounts for a smaller percentage of the total variation than it did in the analysis of absolute cusp area. The eigenvectors for PCI and PCII now have both high and low and positive and negative scores – indicating that they contain information about tooth shape. The first two components for M_1 and M_2 account for 64% and 66% of the total variance, respectively. An examination of eigenvectors indicates that for M_1 PROPCT, ENTPCT and HYPCT contribute positively, while HYLDPCT and METPCT contribute negatively to PCI and METPCT, ENTPCT AND PROPCT contribute positively while HYPCT and HYLDPCT contribute negatively to PCII. For M_2 the pattern is a little different. Here HYLDPCT and METPCT contribute positively to PCI while HYPCT, PROPCT and ENTPCT contribute negatively, and METPCT and ENTPCT contribute positively to PCII while PROPCT, HYLDPCT and HYPCT contribute negatively.

When specimens are plotted along PCI and PCII there is a scattered distribution with no obvious clustering of data points (Figs. 5.13 and 5.14). For M_1, while the Neandertals do tend to fall on the negative side of PCI indicating a relatively large hypoconulid, there is complete overlap between Neandertals and both contemporary and

Upper Paleolithic amHs. The *Homo erectus* specimens do tend to cluster together more than other groups, especially along PCII, and the two early amHs specimens are closer to the *Homo erectus* specimens than they are to other groups. For M_2 the separation of groups is a little bit better for fossil hominids, while the range of variation in contemporary amHs encompass all but the *Homo erectus* and one early amHs specimens. Along PCI, Neandertals tend to fall towards the positive pole, indicating relatively larger hypoconulids while Upper Paleolithic amHs (with smaller hypoconulids) tend to fall towards the negative pole. Along PCII Neandertals tend to fall towards the negative pole, along with the Upper Paleolithic amHs and *Homo erectus* specimens, all of which have relatively large protoconids.

Overall, contemporary amHs exhibit considerable variability in the relative cusp areas of the mandibular molars. The variation in this sample encompasses that of nearly all the other samples. For this reason neither M_1 nor M_2 relative cusp areas appear to be good discriminators between contemporary amHs and Neandertals. They may, however be more useful in separating other fossil hominids, as separation among these samples is better.

TABLE 5.14. Principal component analysis of relative cusp areas in M_1 and M_2

	Absolute Cusp Area				Relative Cusp Area			
	PCI		PCII		PCI		PCII	
	M_1	M_2	M_1	M_2	M_1	M_2	M_1	M_2
Eigenvalues	2.72	2.39	0.81	0.93	1.90	1.93	1.34	1.41
% variance	54.5	47.9	16.2	18.7	38.0	38.6	26.8	28.3
Eigenvectors								
PROPCT[1]	-0.87	-0.84	-0.18	-0.05	0.48	-0.28	0.04	-0.57
METPCT	-0.81	-0.61	-0.04	0.51	-0.14	0.21	0.65	0.58
ENTPCT	-0.74	-0.71	-0.53	-0.52	0.58	-0.57	0.16	-0.10
HYPCT	-0.59	-0.54	0.36	-0.43	0.05	-0.34	-0.74	0.48
HYLDPCT	-0.63	-0.71	0.60	0.47	-0.63	0.65	-0.03	-0.28

[1] See Table 5.10 for abbreviations.

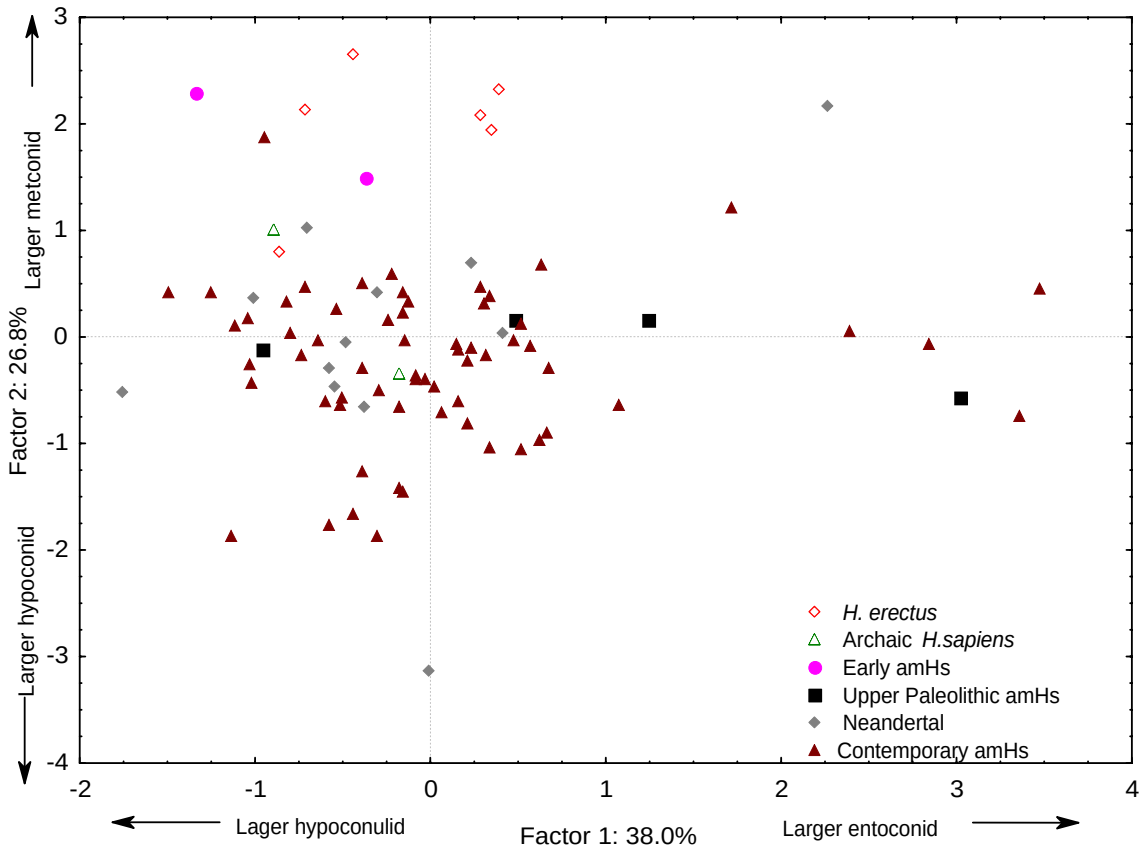


Fig. 5.13. Principal components analysis of M_1 relative cusp areas. Arrows indicate morphology that contribute positively and negatively to Factors 1 and 2.

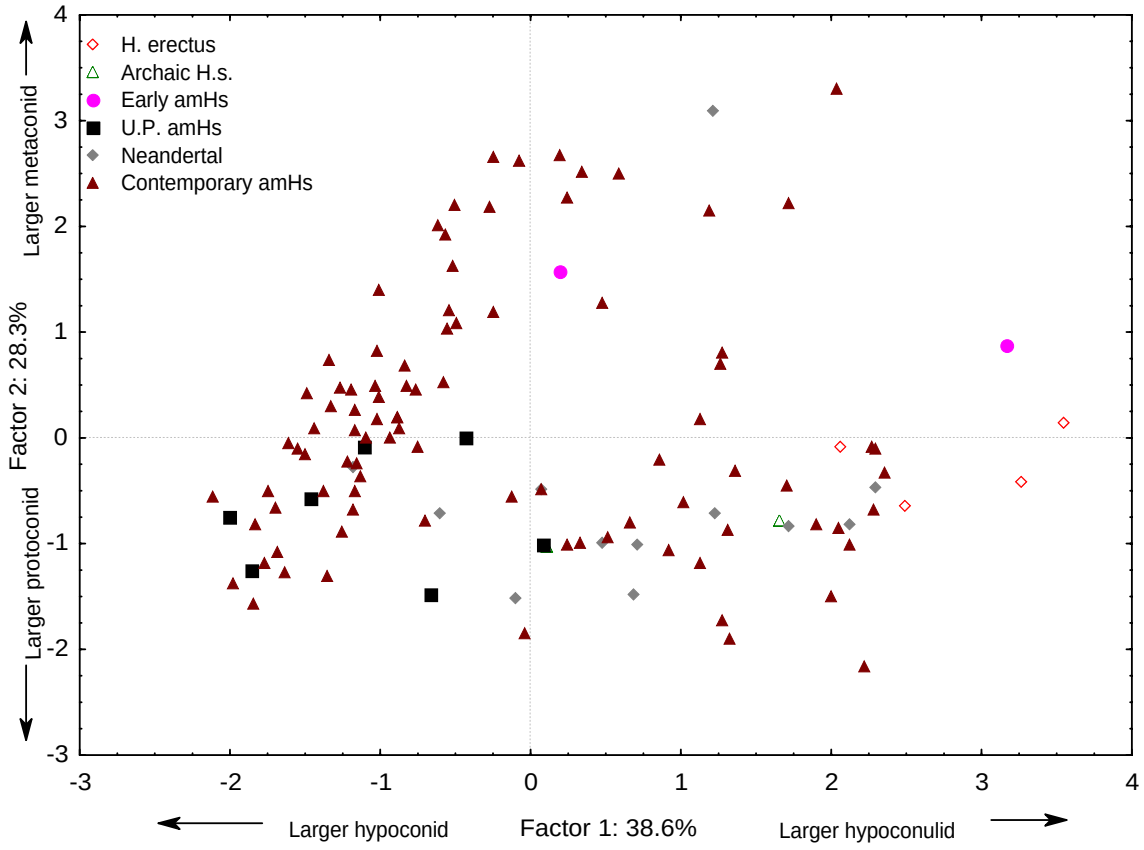


Fig. 5.14. Principal components analysis of M_2 relative cusp areas. Arrows indicate morphology that contribute positively and negatively to Factors 1 and 2.

Occlusal polygon areas and cusp angles

The rationale behind the following analysis of occlusal polygon area and cusp angles is based on personal observations that 1) the cusps of Neandertal molars appear to be relatively close together compared to the condition observed in recent modern humans; and that 2) relative to other human groups the crown shape of Neandertal maxillary molars appears to be skewed buccolingually. To measure the degree to which the cusps are internally placed (an attribute also noted by Tattersall and Schwartz [1999]), an occlusal polygon area was derived from a polygon defined by the tips of each cusp and then expressed as a percent of total crown area. This is the relative occlusal polygon area. To measure the degree to which the tooth shape differs among samples, cusp angles were taken using cusp tips as landmarks.

The analyses of cusp angles and occlusal polygon areas of mandibular molars were hindered by tooth wear, as even a small amount of wear can make it difficult to identify exactly where the individual cusp tips are. This resulted in smaller sample sizes, such that only the Neandertal, contemporary amHs samples and *Homo erectus* could be statistically compared for M_1 and only Neandertal and contemporary amHs could be statistically compared for M_2. Early amHs samples were excluded as tooth wear precluded any measurements that used cusp tips as landmarks.

Tables 5.15 and 5.16 present the descriptive statistics for relative occlusal polygon areas. A Kruskal-Wallis test revealed no significant differences among groups (Bonferroni corrected or uncorrected) for either M_1 and M_2. Inspection of the mean

values for occlusal polygon areas shows them to be quite similar among groups. Figs. 5.15 and 5.16 illustrate the mean and range of variation in each group.

TABLE 5.15. Descriptive statistics for relative occlusal polygon areas of M_1.

	No	X	S.D.	Range
Homo erectus	3	39.0	1.2	37.7-40.0
Neandertal	**11**	**41.1**	**3.0**	**37.1-46.3**
Upper Paleolithic amHs	1	35.6	*	*
Contemporary amHs	30	42.0	2.6	37.1-46.6

TABLE 5.16. Descriptive statistics for relative occlusal polygon areas of M_2

	No	X	S.D.	Range
Homo erectus	2	36.1	*	35.1-37.1
Neandertal	**10**	**41.2**	**2.9**	**36.5-44.8**
Upper Paleolithic amHs	1	25.9	*	*
Contemporary amHs	17	40.3	4.5	28.0-47.9

Tables 5.17 and 5.18 present the descriptive statistics for cusp angles. A Kruskal-Wallis test performed on M_1 cusp angles indicates significant differences among groups for angle D only. Angle D is determined by the placement of the metaconid, entoconid and hypoconulid relative to each other. A Mann-Whitney-U test reveals that this significant difference is attributable to the *Homo erectus*-Neandertal and *Homo erectus* – contemporary amHs comparisons ($p<.05$). However, after the Bonferroni correction is made neither of these comparisons are significant. For M_2 a Kruskal-Wallis test indicates no significant differences in cusp angles between Neandertals and contemporary amHs.

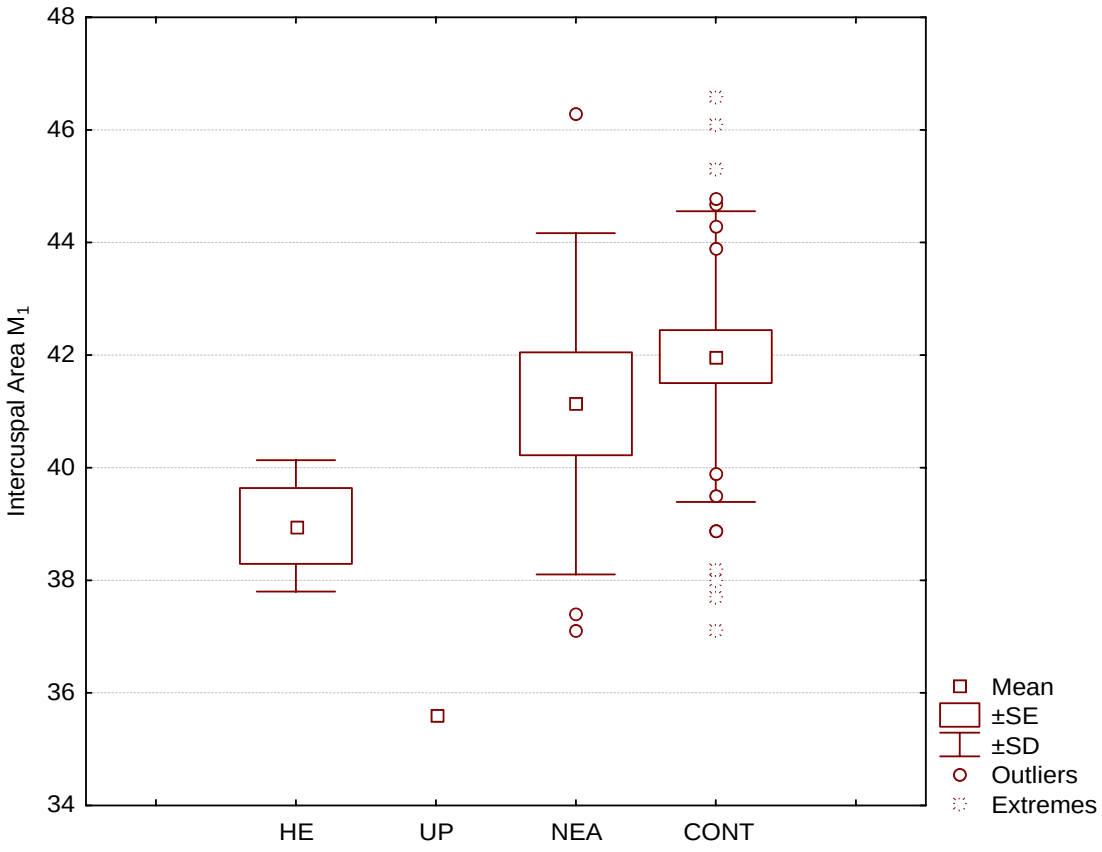


Fig. 5.15. Relative occlusal polygon areas for M_1. The mean values for Neandertals and contemporary amHs are very similar and their ranges of variation overlap completely.

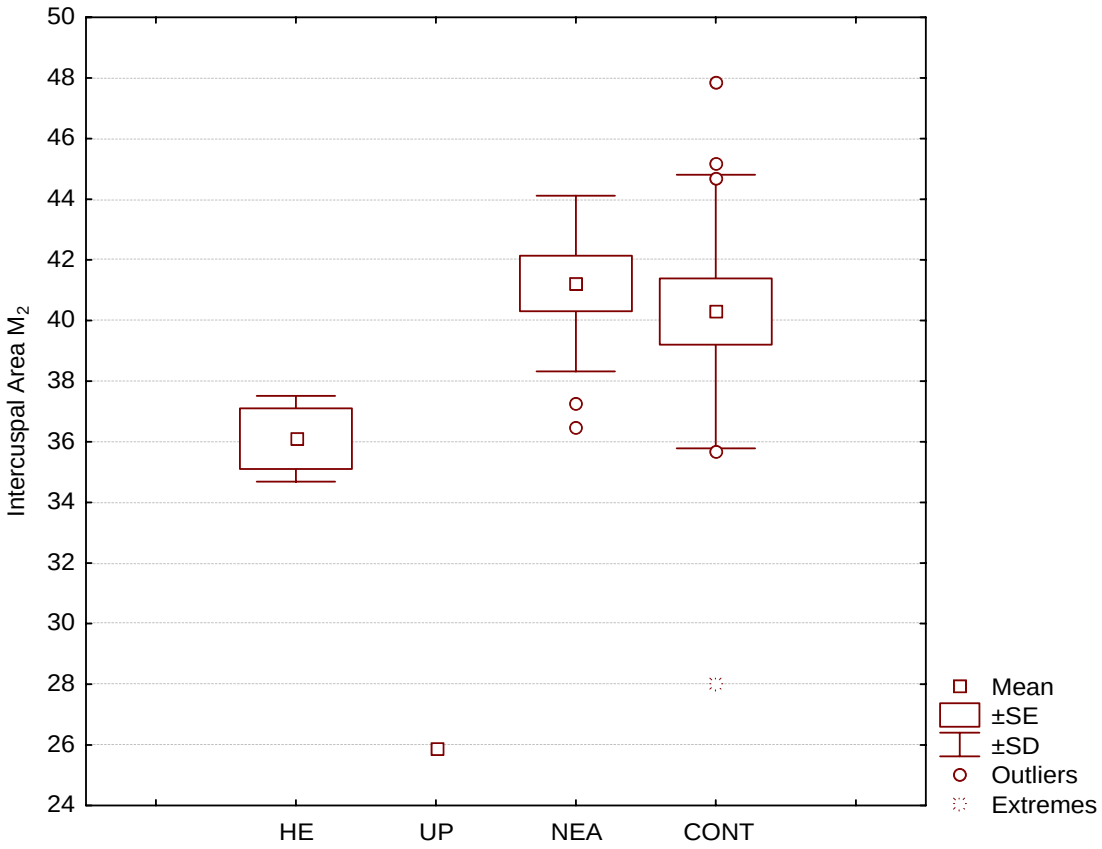


Fig. 5.16. Relative occlusal polygon areas for M_2. The mean values for Neandertals and contemporary amHs are very similar and their ranges of variation overlap completely.

TABLE 5.17. Descriptive statistics for cusp angles of M_1

Angle	A			**B**			C			D			E		
Group	No	Mean	SD	No	Mean	SD	No	Mean	SD	No	Mean	SD	No	Mean	SD
Homo erectus	3	89.3	1.7	3	128.6	12.0	3	103.6	2.9	3	124.3	11.1	3	94.0	3.9
Neandertal	**10**	**96.4**	**5.0**	**10**	**141.8**	**5.5**	**10**	**97.9**	**5.9**	**10**	**109.9**	**5.6**	**10**	**94.0**	**4.7**
U.P. amHs	1	92.8	*	1	137.7	*	1	94.0	*	10	126.7	*	1	89.0	*
Contemporary amHs	19	94.1	5.1	19	141.9	9.6	19	98.4	6.3	19	109.0	8.2	19	96.3	5.5

TABLE 5.18. Descriptive statistics for cusp angles of M_2

Angle	A			**B**			C			D			E		
Group	No	Mean	SD	No	Mean	SD	No	Mean	SD	No	Mean	SD	No	Mean	SD
Homo erectus	1	106.2	*	1	147.0	*	1	107.9	*	1	118.5	*	1	79.9	*
Neandertal	**8**	**99.5**	**9.1**	**8**	**129.9**	**6.6**	**8**	**104.6**	**6.3**	**8**	**114.7**	**7.7**	**8**	**91.4**	**6.3**
U.P. amHs	1	107.1	*	1	121.6	*	1	107.9	*	1	124.1	*	1	79.9	*
Contemporary amHs	9	96.3	9.1	9	131.8	10.0	9	100.4	9.4	9	117.9	13.9	9	93.7	9.2

Summary of mandibular molar morphometrics:

Lower molar shape as described by relative cusp size, cusp angles and occlusal polygon area does not appear to be a particularly useful diagnostic tool for discriminating between contemporary amHs and Neandertals. Univariate and multivariate analyses of these features revealed few significant differences among samples. Although lower molars give the impression of having somewhat compressed cusps, this cannot be confirmed statistically.

Maxillary molars

Relative cusp areas

Relative cusp areas of the maxillary molars are presented in Tables 5.19 and 5.20. In all groups the protocone is the largest of the four cusps. With few exceptions the pattern observed in both M^1 and M^2 is PROPCT>PARPCT>METPCT>HYPCT[3]. Exceptions include archaic *Homo sapiens* M^1, Neandertal M^1, and early amHs M^2. Both early amHs and archaic *Homo sapiens* samples consist of very few individuals and the difference in the pattern may be due to sampling error. In Neandertals the pattern of relative cusp size is PROPCT>PARPCT>HYPCT>METPCT. The larger hypocone (relative to the metacone) observed in Neandertals confirms (quantitatively) that which was observed using the ASUDAS. The Neandertal pattern of relative cusp areas was also observed in early amHs. The pattern in the archaic *Homo sapiens* is

[3] PROPCT, protocone percent of total crown area; PARPCT, paracone percent of total crown area; METPCT, metacone percent of total crown area; HYPCT, hypocone percent of total crown area.

PROPCT>PARPCT=METPCT =HYPCT. The pattern found in contemporary amHs (PROPCT>PARPCT>METPCT >HYPCT) is shared in all samples regardless of geographic origin.

Inspection of the coefficients of variation (CV) shows that, as was the case for mandibular molars, the mesial cusps are generally less variable than are the distal cusps, and M^1 tends more variable in relative cusp size than M^2. For M^1, the hypocone is the most variable of the four cusps in anatomically modern humans, whereas the paracone is the most variable in the Neandertal sample; in *Homo erectus* it is the metacone that is most variable. For M^2, the hypocone is, again, the most variable of the four cusps in the Neandertal, Upper Paleolithic and contemporary amHs samples, while in *Homo erectus* it is the protocone and in early amHs it is the metacone that is most variable. Of course, in both M^1 and M^2 the sample sizes in *Homo erectus* and early amHs are very small and any observed differences may be attributable to sampling error.

The significance of the differences in mean values was examined using Mann-Whitney-U tests. The results of this analysis are presented in Tables 5.21 and 5.22. Statistical comparisons were not made with the archaic *Homo sapiens* sample, which had a sample size of two individuals. As with the mandibular molars, a Bonferroni Correction was applied to the statistical analysis, but uncorrected significant values are also provided in the table.

According to the Bonferroni Corrected significance level (.005) the only significant differences in relative cusp areas are found between Neandertals and

TABLE 5.19. Relative cusp areas of M^1 in fossil and contemporary humans

	PROPCT[1]					PARPCT					METPCT				
	X	N	SD	Range	CV	X	N	S.D	Range	CV	X	N	S.D	Range	CV
HE	31.4	3	1.1	30.2-32.3	3.5	26.0	3	2.3	24.5-28.6	8.8	21.4	3	3.3	17.9-24.3	15.4
EHS	29.5	3	3.1	27.3-33.0	10.5	23.5	3	0.8	22.8-24.4	3.4	19.6	3	0.1	19.5-19.7	0.5
AHS	35.5	2	*	33.4-37.5	*	26.0	2	*	24.3-27.8	*	20.9	2	*	19.7-22.1	*
NEA	**29.7**	**14**	**2.6**	**25.8-33.9**	**8.8**	**25.2**	**14**	**2.3**	**22.0-30.6**	**9.1**	**21.1**	**14**	**1.8**	**18.5-25.5**	**8.5**
UP	30.7	6	1.7	28.0-32.8	5.5	25.9	6	3.9	21.6-31.7	15.1	23.5	6	2.2	20.0-25.4	9.4
CONT	31.0	64	2.1	25.9-35.8	6.8	25.9	64	2.0	22.0-31.9	7.7	22.9	64	1.9	18.0-27.6	8.3

	HYPCT				
	X	N	S.D	Range	CV
HE	21.2	3	2.4	18.5-23.3	11.3
EHS	27.4	3	2.9	24.1-29.6	10.6
AHS	17.6	2	*	16.1-19.1	*
NEA	**24.1**	**14**	**2.1**	**19.0-26.7**	**8.7**
UP	20.0	6	4.0	14.9-25.3	20
CONT	20.2	64	2.4	14.8-25.2	11.9

[1] PROPCT, protocone percent of total crown area; PARPCT, paracone percent of total crown area; METPCT, metacone percent of total crown area; HYPCT, hypocone percent of total crown area.

TABLE 5.20. Relative cusp areas of M^2 in fossil and contemporary humans

	PROPCT[1]					PARPCT					METPCT				
	X	N	S.D	Range	CV	X	N	S.D.	Range	CV	X	N	S.D.	Range	CV
HE	31.0	3	5.9	25.7-37.3	19.0	27.1	3	1.3	25.6-27.9	4.8	22.8	3	3.2	20.3-26.4	14.0
EHS	33.8	3	2.2	31.3-35.2	6.5	25.0	3	1.7	23.5-26.9	6.8	18.7	3	1.8	17.0-20.6	9.6
AHS	27.6	2	*	24.7-30.6	*	24.2	2	*	23.9-24.5	*	24.3	2	*	24.0-24.6	*
NEA	**31.9**	**11**	**2.1**	**29.2-35.7**	**6.6**	**28.4**	**11**	**2.9**	**22.8-32.2**	**10.2**	**21.2**	**11**	**1.7**	**19.5-24.8**	**8.0**
UP	41.7	7	5.4	34.1-47.0	12.9	30.1	7	2.7	24.8-33.5	9.0	19.8	7	3.3	13.6-24.2	16.7
CONT	35.0	79	3.8	28.7-47.9	10.9	29.3	79	2.5	24.0-39.4	8.5	21.0	79	2.5	10.2-28.0	11.9

	HYPCT				
	X	N	S.D.	Range	CV
HE	19.2	3	2.8	16.0-21.3	14.6
EHS	22.5	3	2.1	20.9-24.9	9.3
AHS	24.3	2	*	22.0-26.5	*
NEA	**19.0**	**11**	**3.7**	**10.2-24.6**	**19.5**
UP	8.5	7	4.6	3.9-16.9	54.1
CONT	14.7	79	5.4	3.5-36.2	36.7

[1] See Table 5.19 for abbreviations.

TABLE 5.21. Between group comparisons of M^1 relative cusp areas (significance values based on Mann Whitney U non parametric tests[1])

	PROPCT[2]					PARPCT				
	HE	EHS	NEA	UP	REC	HE	EHS	NEA	UP	REC
HE	---					---.				
EHS	N.S.	---				*	---			
NEA	**N.S.**	**N.S.**	**---**			**N.S.**	**N.S.**	**---**		
UP	N.S.	N.S.	**N.S.**	---		N.S.	N.S.	**N.S.**	---	
REC	N.S.	N.S.	**N.S.**	N.S.	---	N.S.	*	**N.S.**	N.S.	---

	METPCT					HYPCT				
	HE	EHS	NEA	UP	REC	HE	EHS	NEA	UP	REC
HE	---					---				
EHS	N.S.	---				*	---			
NEA	**N.S.**	*****	**---**			**N.S.**	**N.S.**	**---**		
UP	N.S.	*	*****	---		N.S.	*	*****	---	
REC	N.S.	**	*******	N.S.	---	N.S.	**	*******	N.S.	---

TABLE 5.22. Between group comparisons of M^2 relative cusp areas (significance values based on Mann Whitney U non parametric tests[1])

	PROPCT[2]					PARPCT				
	HE	EHS	NEA	UP	REC	HE	EHS	NEA	UP	REC
HE	---					---				
EHS	N.S.	---				N.S.	---			
NEA	**N.S.**	**N.S.**	**---**			**N.S.**	**N.S.**	**---**		
UP	N.S.	N.S.	**	---		N.S.	*	**N.S.**	---	
CONT	N.S.	N.S.	**	**	---	N.S.	*	**N.S.**	N.S.	---

	METPCT					HYPCT				
	HE	EHS	NEA	UP	REC	HE	EHS	NEA	UP	REC
HE	---					---				
EHS	N.S.	---				N.S.	---			
NEA	**N.S.**	**N.S.**	**---**			**N.S.**	**N.S.**	**---**		
UP	N.S.	N.S.	N.S.	---		*	*	******	---	
CONT	N.S.	N.S.	N.S.	N.S.	---	N.S.	**	******	**	---

[1] N.S., not significant; * significant at .05 (uncorrected); ** significant at .01 (uncorrected); *** significant at corrected Bonferroni level (.005)
[2] See Table 5.19 for abbreviations

contemporary amHs. These are few, and include METPCT and HYPCT for M^1. Compared to the mean value observed in contemporary amHs, the Neandertal hypocone and metacone are relatively large. Relative to the Upper Paleolithic and contemporary amHs, Neandertals also exhibit a larger M^2 hypocone, although this is not significant at the corrected significance level. Overall, the pattern of relative cusp size observed in Neandertals is most similar to that observed in early amHs.

Results of a Principal Component Analysis for both absolute and relative cusp areas of M^1 and M^2 are presented in Table 5.23. In the PCA of absolute cusp areas for M_1, the first principal component (PCI) accounts for approximately 76% of the total variance. For M_2, PCI accounts for approximately 66% of the total variance. In both cases the eigenvectors have the same sign and approximately equal weight is given to each of the cusps suggesting that the major separating effect is size.

For relative cusp area the resulting PCIs account for a smaller percentage of the total variation than they did in the analysis of absolute cusp area. The eigenvectors for PCI and PCII have both high and low and positive and negative scores – indicating that they contain information about tooth shape. For M^1 and M^2 the first two components account for approximately 74% and 83% of the total variance (respectively). An examination of eigenvectors indicates that for M^1 the cusp areas that make up the trigone (PROPCT, PARPCT, METPCT) contribute positively to PCI, while the hypocone (HYPCT) contributes negatively. For M^2 PROPCT and PARPCT contribute positively (nearly equally so) while the HYPCT and (less so) METPCT contribute negatively. These differences correspond to differences in the mesial and distal portions of the tooth,

respectively. For PCII the METPCT makes a large positive contribution and the PARPCT a much smaller one, while the PROPCT and HYPCT both contribute negatively. These differences correspond to differences in the buccal and lingual portions of the tooth respectively.

TABLE 5.23. Principal components analysis of absolute and relative cusp areas in M^1 and M^2

	Absolute Cusp Area				Relative Cusp Area			
	PCI		PCII		PCI		PCII	
	M^1	M^2	M^1	M^2	M^1	M^2	M^1	M^2
Eigenvalues	3.0	2.63	0.47	0.82	1.77	2.20	1.18	1.10
% variance	75.6	65.8	11.8	20.4	44.2	55.1	29.6	27.7
Eigenvectors								
PROPCT	-0.52	0.51	0.12	-0.42	0.32	-0.57	0.73	-0.20
PARPCT	-0.51	0.56	0.30	-0.21	0.48	-0.51	-0.12	0.03
METPCT	-0.51	0.54	0.35	0.04	0.27	0.09	-0.67	0.94
HYPCT	-0.46	0.36	-0.88	0.87	-0.77	0.64	-0.00	-0.28

When specimens are plotted along PCI and PCII (Figs. 5.17 and 5.18) the distribution is scattered with no clear separation of the groups and a substantial degree of overlap. However, there are some trends that can be discerned. For M^1 Neandertals tend to fall toward the negative pole of PCI while contemporary amHs tend to fall toward the positive pole. This reflects the relatively large hypocone observed in Neandertals and the relatively large paracone in contemporary amHs. Early amHs, with the largest relative hypocone, occupy a position opposite that of contemporary modern humans along PCI. Like Neandertals they fall toward the negative pole of PCI. *Homo erectus* and Upper

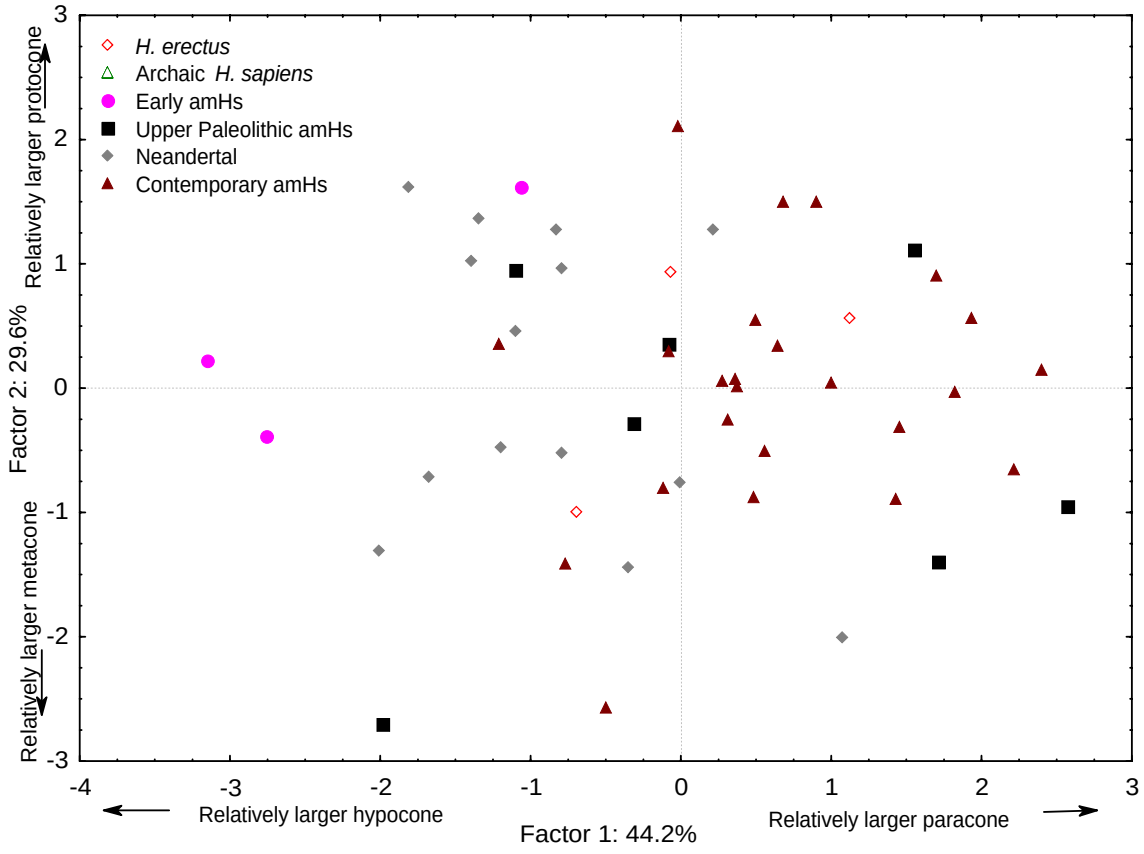


Fig. 5.17. Plot of the first (Factor 1) and second (Factor 2) principal components generated from the relative cusp area data of fossil and contemporary human M^1.

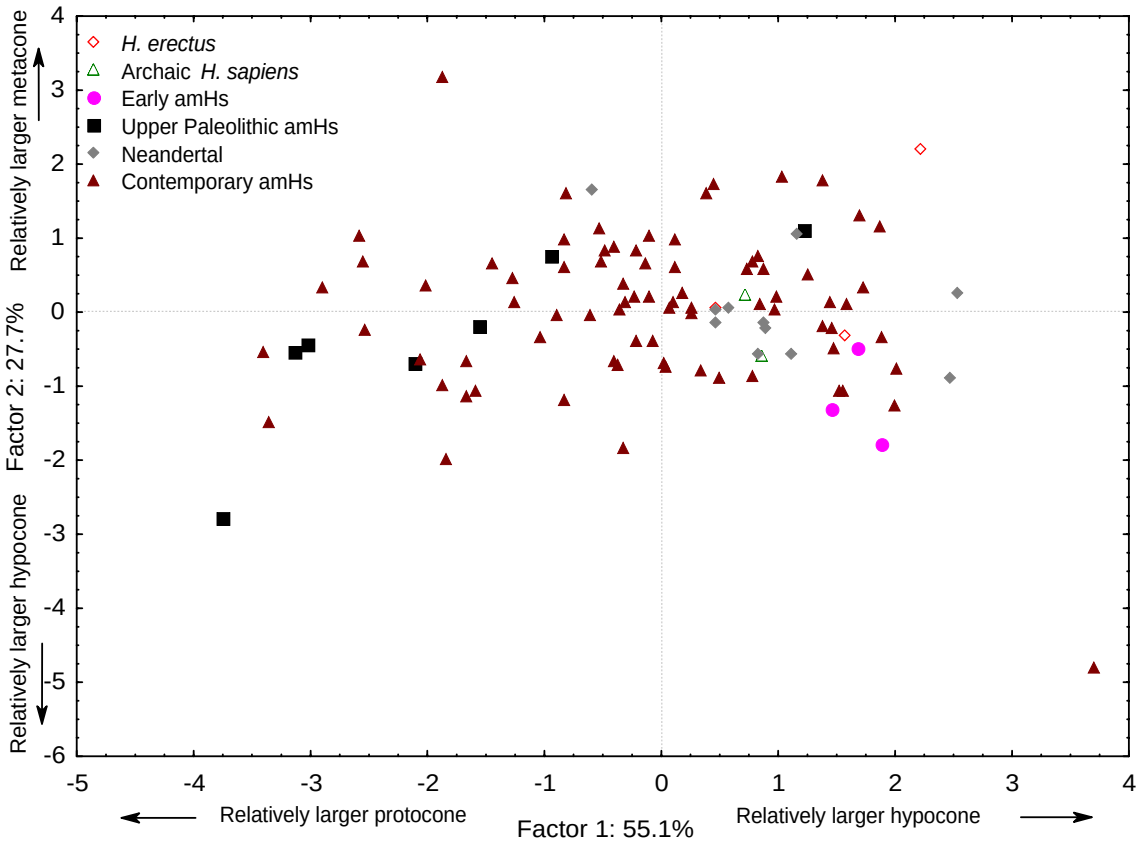


Fig. 5.18. Plot of the first (Factor 1) and second (Factor 2) principal components generated from the relative cusp area data of fossil and contemporary human M^2.

Paleolithic amHs are encompassed within the variation of Neandertals and amHs. Along PCII there is a complete intermixing of groups.

For M^2, with one exception, Neandertals fall toward the positive pole of PCI together with amHs and *Homo erectus* individuals. This reflects the relatively large hypocone in each sample. Nearly all the Upper Paleolithic amHs individuals fall on the opposite end of PCI reflecting their relatively large protocone, while the contemporary amHs is extremely variable – encompassing nearly all the fossil hominid variation. For PCII, Neandertals and Early amHs fall more toward the negative pole while the rest of the samples are more variable.

Differences in relative cusp area among fossil hominid and modern groups can be largely attributed to differences in the relative size of the distal portion of the tooth. The hypocone appears to be the primary contributor to these differences. Information on the relative cusp areas of other cusps are less useful for discriminating among samples.

Relative occlusal polygon area

The relative sizes of the occlusal polygon area are presented in Tables 5.24 and 5.25. It is clear that the maxillary occlusal polygon area in the Neandertal sample is considerably smaller than it is in other groups. This is especially so for M^1. These differences can be appreciated graphically from Figs. 5.19 and 5.20.

A Kruskal-Wallis test revealed significant differences among groups. Using the Bonferroni correction ($p<.016$) to control for multiple comparisons, subsequent Mann-Whitney U tests of pairs showed that the occlusal polygon area of the Neandertal M^1 is significantly different from that of both early amHs and contemporary amHs. A

significance test of the differences between Neandertals and *Homo erectus* and Upper Paleolithic amHs could not be performed because each sample consisted of only two individuals. However, inspection of the mean values shows they are much more similar to early and contemporary amHs then they are to Neandertals. Mann-Whitney U tests also revealed significant (corrected) differences between Neandertals and contemporary amHs in the M^2 occlusal polygon areas. However, differences between Neandertals and other fossil hominids were not statistically significant.

TABLE 5.24. Relative occlusal polygon areas among human groups M^1

	No	Mean	SD	Range
Homo erectus	2	32.9	2.9	30.8-35.0
Early amHs	3	33.1	3.5	29.6-36.6
Neandertal	**12**	**26.8**	**1.8**	**24.5-30.5**
Upper Paleolithic amHs	2	34.3	3.5	31.8-36.8
Contemporary amHs	24	37.5	5.4	27.0-50.4

TABLE 5.25. Relative occlusal polygon areas among human groups M^2

	No.	Mean	SD	Range
Homo erectus	3	32.6	2.7	29.8-35.1
Early amHs	3	30.4	2.5	27.9-33.0
Neandertal	**9**	**29.1**	**3.1**	**23.6-34.2**
Upper Paleolithic amHs	5	29.7	2.8	25.8-32.8
Contemporary amHs	34	36.0	4.4	27.4-44.6

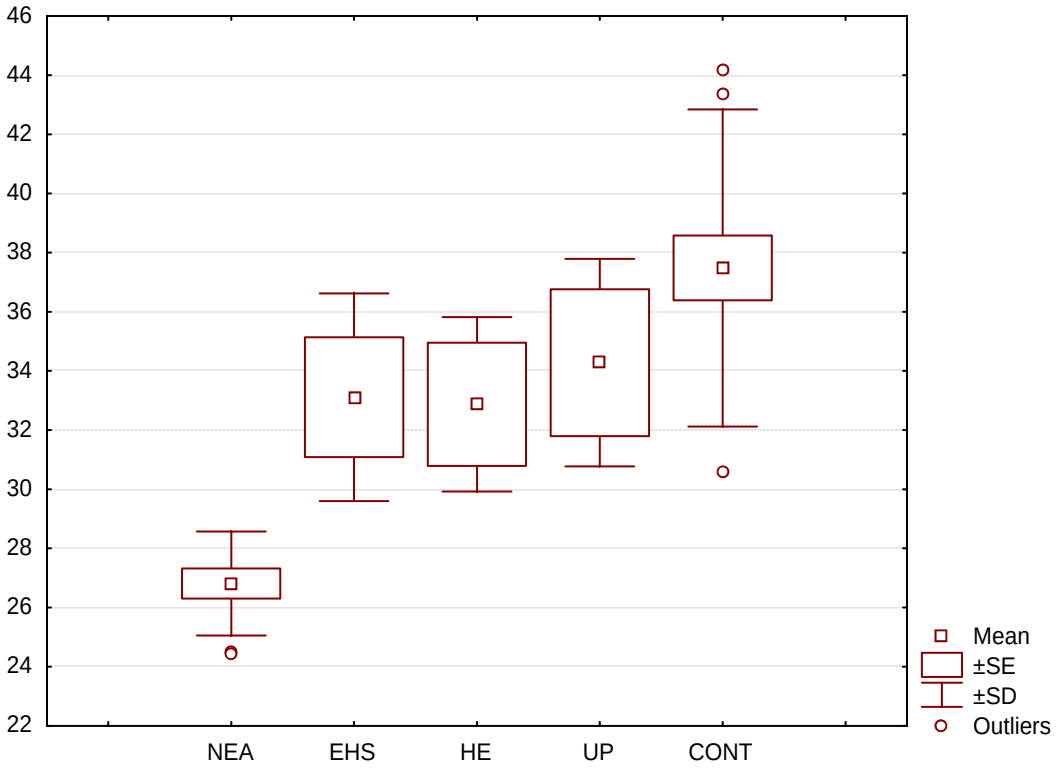


Fig. 5.19. Plot of relative occlusal polygon areas for contemporary and fossil human M^1.

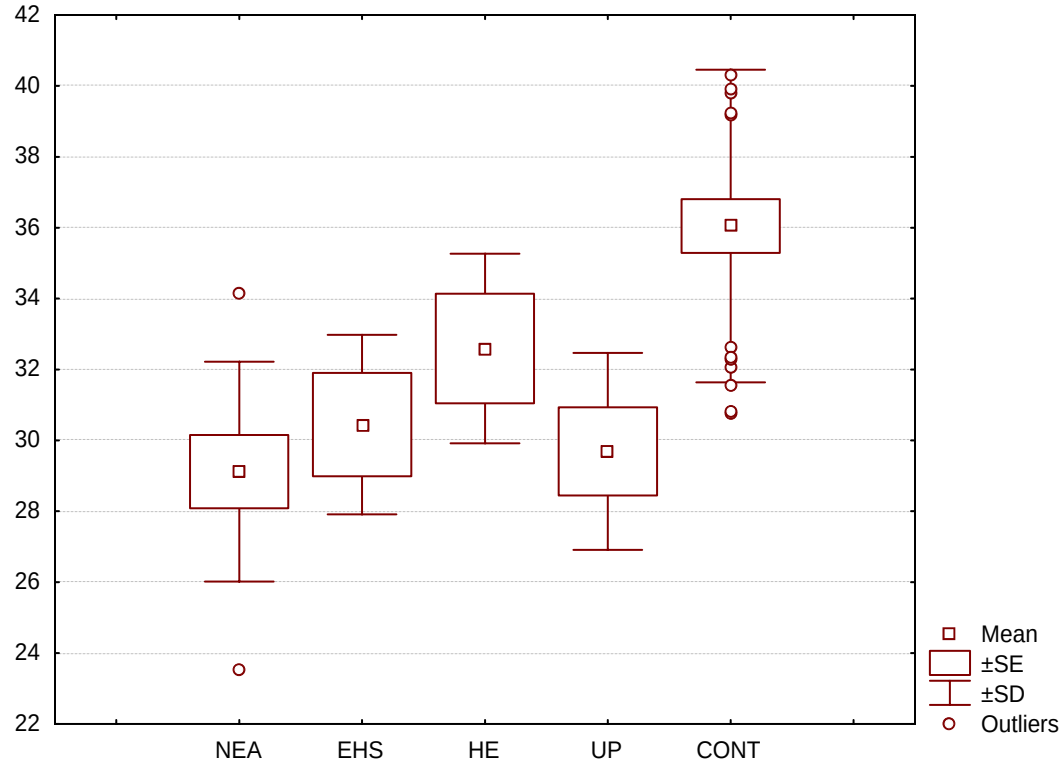


Fig. 5.20. Plot of relative occlusal polygon areas for contemporary and fossil human M^2.

Cusp angles

In general, all groups are characterized by an M^1 that tends to be rhomboid in shape such that angles A and C are larger than angles B and D. Mean values for these angles (Tables 5.26 and 5.27) shows that in Neandertals angle C is relatively large, while angles B and D are relatively small when compared to other samples.

When compared statistically (Tables 5.28 and 5.29) angle A – represented by the cusp tips of the paracone, protocone and hypocone – is the most conservative. The differences among groups are small and not statistically significant. The remaining three cusp angles appear to be responsible for the observed differences in tooth shapes. Using a Bonferroni correction ($p<.005$) Neandertals show significant differences in angles B, C and D when compared to contemporary amHs. However, none of the differences in cusp angles between Neandertals and early amHs are statistically significant. A significance test of the differences between Neandertals and *Homo erectus* and Upper Paleolithic amHs could not be performed because each sample consisted of only two individuals. However, inspection of the mean values shows they are more similar to early and contemporary amHs then they are to Neandertals.

The tooth shape differences observed in the M^1 are not as obvious in M^2 and the M^2 pattern is somewhat different from that observed in M^1. For M^2 angle B – represented by the cusp tips of the protocone, paracone and metacone – is the least variable, and the differences among samples are small and not statistically significant. According to the Bonferroni correction, the only significant angular difference was found between Neandertals and contemporary amHs for angle D.

TABLE 5.26. Descriptive statistics for cusp angles in M^1 in fossil and contemporary humans

Angle	A			B			C			D		
Group	n	X	SD	n	X	SD	n	X	SD	n	X	SD
Homo erectus	2	105.3	*	2	75.2	*	2	96.8	*	2	82.0	*
Early amHs	3	106.0	9.7	3	72.6	1.4	3	104.9	3.2	3	76.5	8.9
Neandertal	**10**	**106.4**	**5.0**	**10**	**65.1**	**6.9**	**10**	**120.9**	**10.1**	**10**	**67.7**	**7.1**
U.P. amHs	2	105.8	*	2	70.6	*	2	110.3	*	2	73.3	*
Contemporary amHs	24	101.3	10.1	24	74.2	4.0	24	106.1	5.5	24	78.4	7.7

TABLE 5.27. Descriptive statistics for cusp angles in M^2 in fossil and contemporary humans

Angle	A			B			C			D		
Group	n	X	SD	n	X	SD	n	X	SD	n	X	SD
Homo erectus	3	97.3	3.2	3	74.9	3.9	3	108.1	0.6	3	79.7	6.4
Early amHs	3	107.6	6.6	3	73.0	3.4	3	107.4	1.0	3	71.9	3.0
Neandertal	**9**	**105.5**	**5.1**	**9**	**69.5**	**6.5**	**9**	**112.9**	**7.3**	**9**	**72.2**	**5.4**
U.P. amHs	5	77.9	15.4	5	66.3	3.9	5	123.2	8.8	5	92.6	9.4
Contemporary amHs	30	94.0	12.5	30	70.0	10.8	30	108.8	11.4	30	87.2	12.3

TABLE 5.28. Between group comparisons of cusp angles of M^1 (significance values based on Mann Whitney U non parametric tests[1])

	<A			**<B**		
	EHS	NEA	CONT	EHS	NEA	CONT
EHS	---			---		
NEA	**N.S.**	---		**N.S.**	---	
CONT	N.S.	N.S.	---	N.S.	***	---

	<C			**<D**		
	EHS	NEA	CONT	EHS	NEA	CONT
EHS	---			---		
NEA	*	---		**N.S.**	---	
CONT	N.S.	***	---	N.S.	***	---

TABLE 5.29. Between group comparisons of cusp angles of M^2 (significance values based on Mann Whitney U non parametric tests[1])

	<A			**<B**		
	EHS	NEA	CONT	EHS	NEA	CONT
EHS	---			----		
NEA	**N.S.**	---		**N.S.**	---	
CONT	*	**	---	N.S.	N.S.	---

	<C			**<D**		
	EHS	NEA	CONT	EHS	NEA	CONT
EHS	---			---		
NEA	**N.S.**	---		**N.S.**	---	
CONT	N.S.	N.S.	---	*	***	---

[1] N.S., not significant; * significant at .05 (uncorrected); ** significant at .01 (uncorrected); *** significant at corrected Bonferroni level (.005)

A PCA of cusp angles on M^1 and M^2 indicates that the first two factors account for approximately 90% of the total variance (Table 5.30). For M^1, angles A and C contribute positively to PCI, while angles B and D contribute negatively. This indicates that PCI describes the buccolingual skew of the rhomboid. Figure 5.21 illustrates how teeth at the opposite poles of PCI have very different shapes. Teeth toward the negative pole are more square in outline and teeth toward the positive pole are more rhomboid. For M^2 angles B and D contribute positively to PCI while angles A and C contribute negatively. In this case PCI still accounts for the buccolingual skew of the rhomboid but teeth toward the positive pole are more square and teeth toward the negative pole are more skewed (Fig. 5.22).

For PCII the identical pattern is found in M^1 and M^2. In this case, angles A and B contribute positively while C and D contribute negatively. Angles A and B represent the mesial portion of the tooth and angles C and D represent the distal portion, indicating that PCII represents the degree to which the shape of the rhomboid is narrower distally and wider mesially. This is illustrated by plotting specimens at either end of the ranges of variation along this factor. Teeth that are wider distally occupy a positive position along PCII and teeth that are narrower distally occupy a negative position (Figs. 5.21 and 5.22). The distribution of specimens along PCI and PCII are somewhat different for M^1 and M^2. When the M^1 cases are projected on the factor plane for PCI and PCII it is apparent that, compared to other samples, Neandertal M^1s are more buccolingually skewed. Recent modern humans, on the other hand, have an outline that is comparatively more square

(angles are closer to 90 degrees) than in other groups. The groups separate out fairly well along PCI with Neandertals falling predominantly toward the positive pole and modern and other groups falling toward the negative pole (albeit with some overlap). Along PCII there appears to be little pattern to the data; however, closer inspection shows that Neandertals tend to fall toward the negative pole indicating that the M^2 rhombus is more narrow distally than it is mesially. Recent humans, on the other hand, are scattered along PCII with little pattern to their distribution.

For M^2 when the cases are projected on the factor plane for PCI and PCII Neandertals fall predominantly in the upper left hand corner of the graph, expressing its buccolingually skewed rhomboid shape that tends to be wider distally than mesially. The early modern and *Homo erectus* fossils also cluster with the Neandertal specimens. The Upper Paleolithic group occupies a position opposite that of the Neandertals in the lower half and primarily right side of the graph, indicating that the tooth shape is very different (more square and distally narrower) from that of Neandertals. The modern humans show little pattern and are scattered along the axes of both PCI and PCII.

TABLE 5.30. Percentage contribution to total variance and eigenvector scores of the first and second principal components derived from cusp angles

	M^1		M^2	
	PCI	PCII	PCI	PCII
Eigenvalues	2.6	1.08	2.3	1.3
% variance	63.9	27.1	57.1	32.9
Eigenvectors				
Angle A	0.64	0.76	-0.74	0.62
Angle B	-0.86	0.26	0.76	0.51
Angle C	0.76	-0.62	-0.67	-0.68
Angle D	-0.90	-0.24	0.83	-0.45

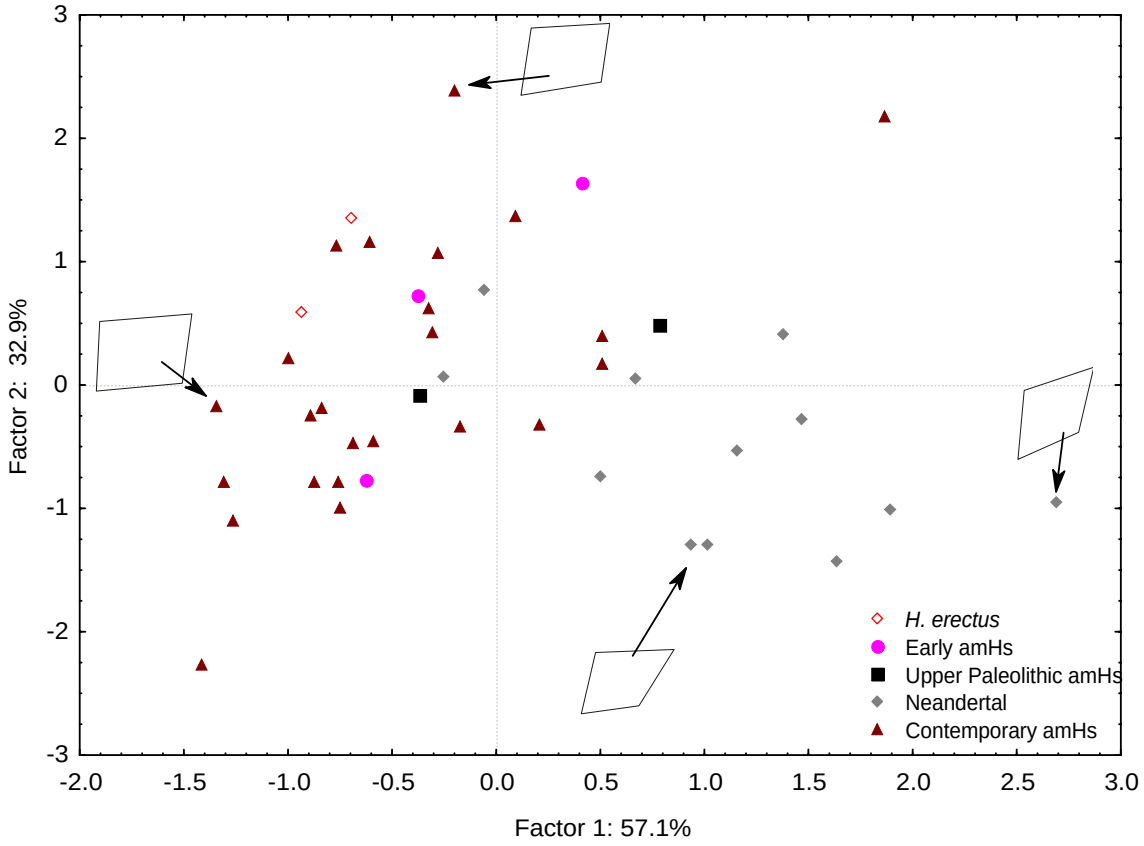


Fig. 5.21. Plot of the first and second principal components generated from cusp angle data in M^1. Polygons indicate shape associated with particular individuals at opposite ends of the axes.

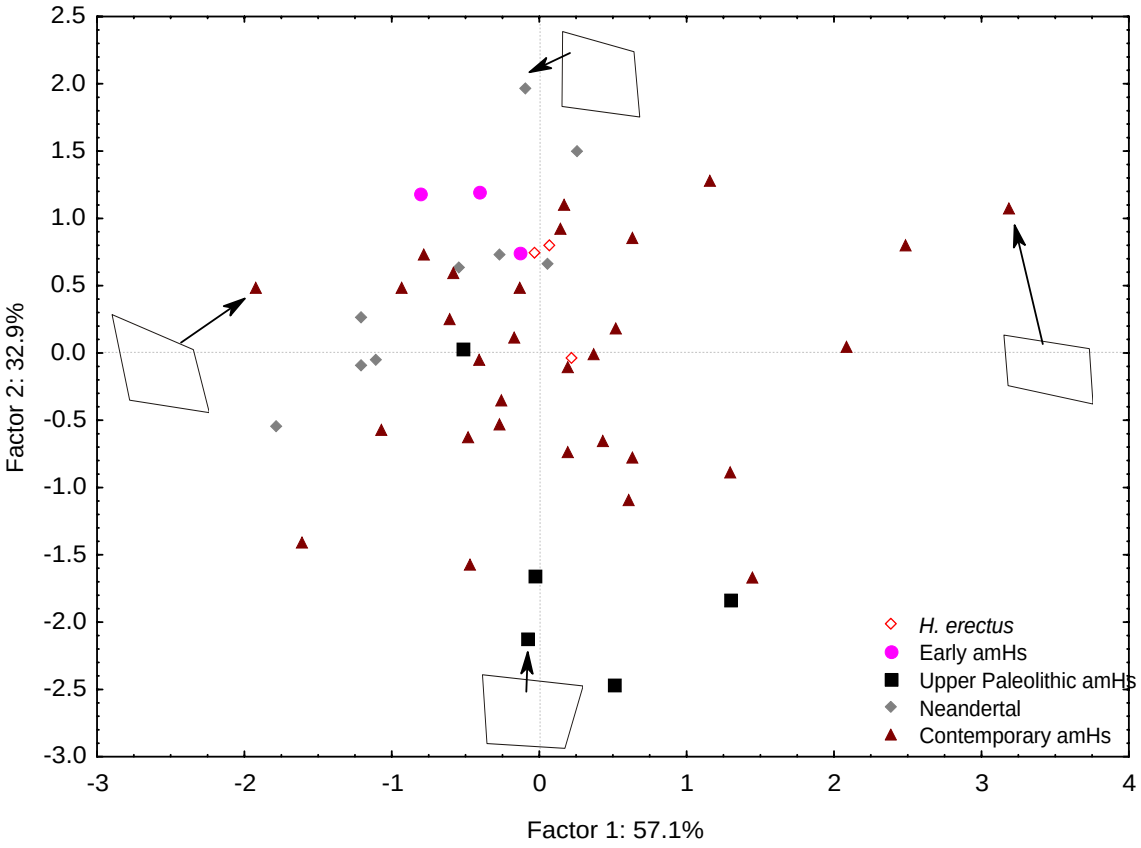


Fig. 5.22. Plot of the first (Factor 1) and second (Factor 2) principal components generated from cusp angle data in M^2. Polygons indicate shape associated with particular individuals at opposite ends of the axes.

Summary of maxillary molar morphometrics

The morphometric analysis of maxillary molars reveals interesting differences between Neandertals and fossil and contemporary human groups. Univariate and multivariate analyses of these features revealed significant differences among samples in relative cusp areas, in relative occlusal polygon area and in cusp angles. These differences are especially notable in M^1.

It is difficult to assess the phylogenetic significance of the occlusal polygon area and cusp angles for several reasons. First, although some differences were shown to be highly significant between Neandertals and contemporary amHs, it was not possible to conduct a reliable statistical test of the significance in other fossil hominids because of small sample sizes. Second, the Neandertal teeth that could be used for this portion of the analysis came predominantly from one site (Krapina), of which a high percentage are unerupted and/or unworn. Few of the modern teeth were completely unworn and it is conceivable that even minimal amounts of wear could affect placement of cusp tips. A study using teeth of juvenile contemporary amHs (those with newly erupted M^1 and/or M^2) would be useful in addressing this issue.

Although possible, it is unlikely that differences in relative cusp areas between Neandertals and contemporary amHs are responsible for the skewed crown shape observed in the Neandertal sample. A simple observation of the early amHs and *Homo erectus* teeth show that they possess a similar pattern in relative cusp size (large hypocone relative to the metacone), but that they do not share the distinctive shape

observed in Neandertals. A larger sample of unworn teeth is needed before the significance of this feature can be determined.

Mandibular second premolar

Crown indices

The crown index (CI=BL/MD x 100) expresses the gross shape of the tooth crown. A CI of 100 indicates a square tooth. A score greater than 100 indicates a tooth that is more rectangular in a buccolingual direction, while a score less than 100 indicates a tooth that is more rectangular in a mesiodistal direction. Here, I briefly describe the results of a simple analysis of tooth crown indices for later comparison with results from the Fourier analysis. Crown indices were derived from measurements taken directly from the specimens using digital calipers. Measurements were taken twice and the averages of first and second scorings were used. If both antimeres were present the left and right sides were averaged.

Crown indices obtained for the samples are presented in Table 5.31. A review of the CI's indicates that in all samples P_4s are rectangular in a buccolingual direction. Some of the groups have a more buccolingually expanded P_4 (Neandertals, *Homo erectus* and Upper Paleolithic amHs) while others are less so (Archaic *Homo sapiens*, early and contemporary amHs). A non-parametric test of the group means indicates that significant differences among samples exist. Subsequent Mann-Whitney-U tests reveal that the comparisons that are responsible are the contemporary amHs-*Homo erectus* and contemporary amHs-Neandertal comparisons. However, using the Bonferroni correction

($p<.003$) these differences are no longer significant. Moreover, the range observed in modern humans encompasses the variation observed in all other groups.

TABLE 5.31 Crown indices in P_4 of contemporary and fossil humans

	N	Means	S.D	Range
Homo erectus	9	123.7	9.5	109.6-139.0
Archaic *Homo sapiens*	2	113.2	*	103.4-123.0
Neandertal	**11**	**124.0**	**12.0**	**104.4-139.3**
Early amHs	1	105.2	*	*
Upper Paleolithic amHs	10	122.0	10.1	106.8-137.7
Contemporary amHs	125	116.6	7.0	100.3-137.5

Crown contour: Elliptic Fourier analysis

The unusual Neandertal P_4 shape cannot be captured by simple crown indices. Therefore, to quantify the shape differences observed in Neandertal and amHs the occlusal outlines of the P_4 were captured and then transformed using Elliptic Fourier Analysis as described in the Methods chapter. The analysis is based on a total of 8 *Homo erectus*, 3 archaic *Homo sapiens*, 4 early amHs, 6 Upper Paleolithic amHs, 95 contemporary amHs, and 20 Neandertal P_4s.

The mean crown shapes for each group are shown in Fig. 5.23. Compared to that of the other samples, the Neandertals P_4 mean shape is asymmetrical. In addition, the lingual portion of the tooth tends to be mesiodistally narrower relative to the buccal portion. In contrast, the mean shapes from each of the non-Neandertals groups are remarkably symmetrical. In early amHs the lingual portion is actually wider than the buccal portion – the opposite of that observed in Neandertals.

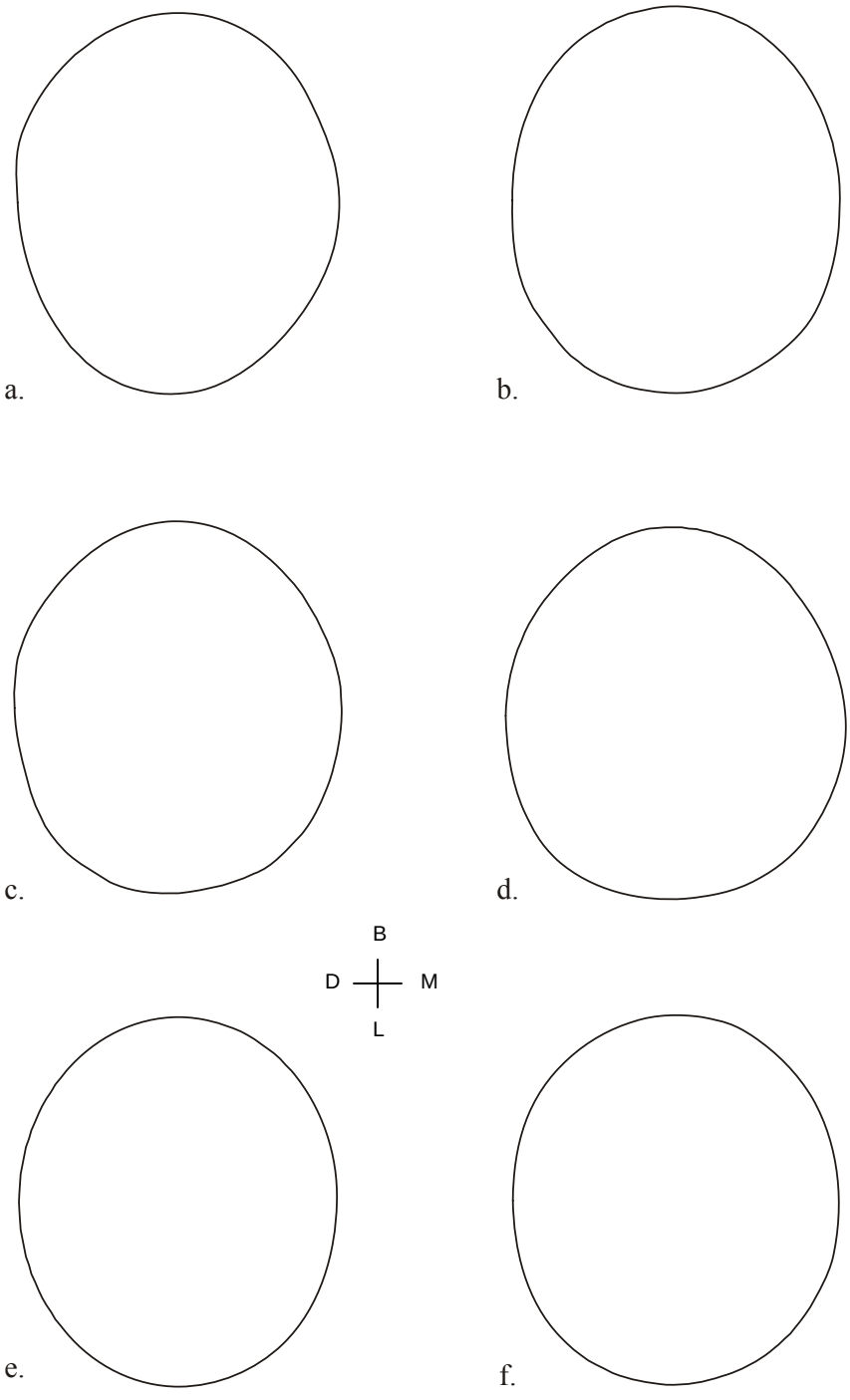


Fig. 5.23. Mean P4 shapes (left) for Neandertals (a); archaic *Homo sapiens* (b); *Homo erectus* (c); early amHs (d); Upper Paleolithic amHs (e); and contemporary amHs (f) based on average elliptic Fourier descriptors. Symbol indicates orientation of the teeth: B: buccal; M: mesial; L: lingual; D: distal.

Principal components analysis

A principal component analysis of the of the matrix of descriptors for 136 teeth shows the major trends of variation in the data. The results are presented in Table 5.32. Significant eigenvalues (>1.0) are listed together with their contribution to the total variance. Together these 11 factors account for 85% of the total variation. Individually each factor's contribution is fairly low. The first two principal components account for 15.4 and 11.9% of the variation, respectively, for a total of 27% of the total cumulative variation.

TABLE 5.32. Significant eigenvalues (>1.0) and their contribution to total variance

	Eigenvalue	% Total variance	Cumulative Eigenvalue	Cumulative %
1	4.46	15.37	4.46	15.37
2	3.47	11.98	7.93	27.35
3	2.87	9.88	10.80	37.23
4	2.48	8.54	13.28	45.78
5	2.07	7.14	15.35	52.92
6	1.93	6.65	17.28	59.57
7	1.81	6.23	19.08	65.81
8	1.63	5.62	20.71	71.43
9	1.55	5.33	22.26	76.76
10	1.32	4.54	23.58	81.30
11	1.06	3.66	24.64	84.96

Figure 5.24 displays the individuals arrayed according to the magnitudes of their projections onto the first two principal component axes computed from the total data set. With one exception Neandertals all have positive eigenvalues for PCI and fall toward the positive pole. To ascertain what this indicates, I examined the Neandertal specimens with the highest values for PCI. Not surprisingly (based on the mean shapes described

above) these teeth (Tabun, Le Moustier and Krapina D50) possess a strongly asymmetrical crown contour. This asymmetry most likely leads to a truncation of the mesiolingual lobe, which in turn, results in a tooth with a smaller lingual than buccal breadth. The single Neandertal P_4 that has a negative eigenvalue for PCI (Spy 2) is a symmetrical tooth with a relatively broad lingual breadth.

The contemporary modern humans are scattered randomly, occupying positions at all four extremes on the two axes. The individual with the highest positive value for PCI (a contemporary amHs from India) is an outlier among all groups examined. This tooth is somewhat asymmetrical with a notably narrow lingual cusp relative to the buccal cusp. The individual with the highest negative value for PCI is a contemporary amHs from West Africa. This tooth is a symmetrical tooth with an exceptionally wide lingual breadth. A tooth sampled from a position in the middle is a Neandertal tooth from Krapina (Mandible D), it is symmetrical with a lingual cusp that approximates the width of the buccal cusp. Based on this it is unclear whether PCI is describing the asymmetry of the tooth or the relative width of the lingual cusp. However, examination of the teeth at opposite poles of PCII is very informative in this regard. A tooth that has the highest negative score for PCII is from India. It exhibits an markedly narrow lingual cusp but is symmetrical. This suggests that asymmetry, rather than relative width of the lingual cusp, is contributing to positive scores along PCI.

Principal component II is not easily interpreted, as there is little pattern to how the individuals are arrayed along this axis. As was the case for PCI, the contemporary amHs.

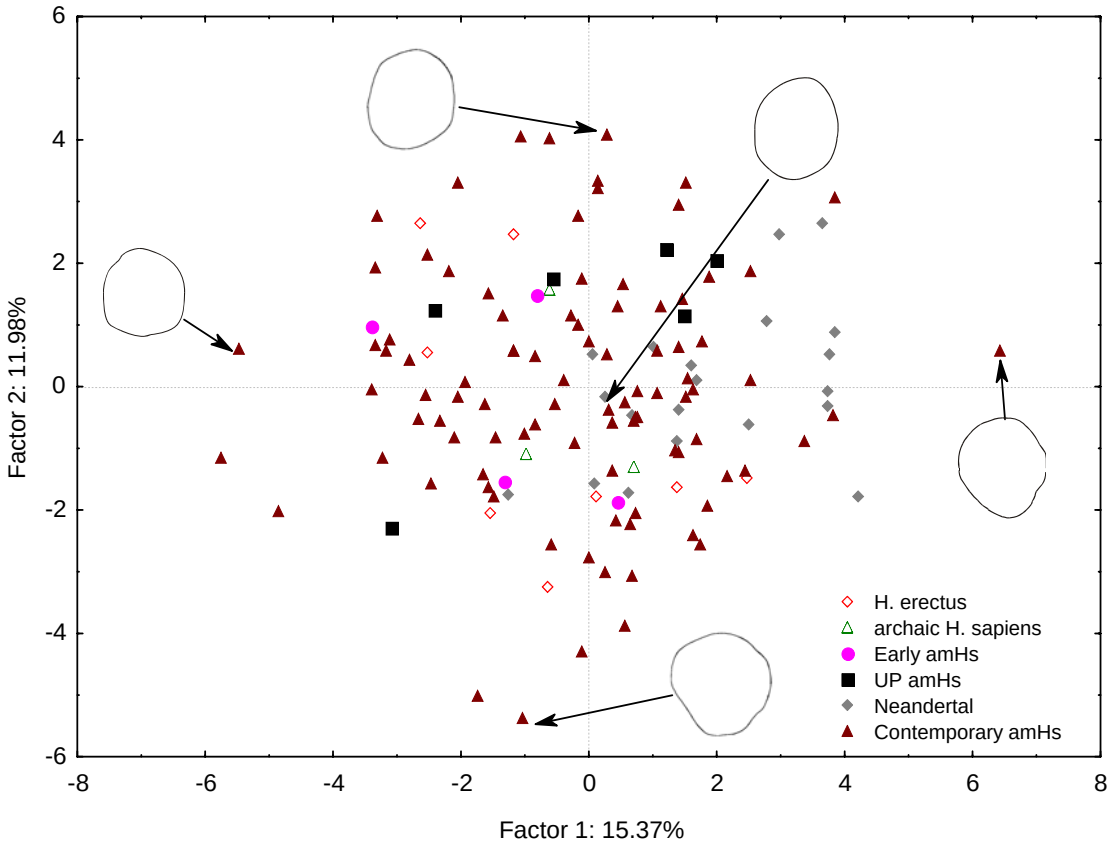


Fig. 5.24. Plot of individuals arrayed according to the magnitudes of their projections onto the first two principal component axes computed from the total data set. Drawings indicate the tooth shape associated with particular individuals at opposite ends of the axes.

fall at the two extremes with both high negative and high positive scores. All other groups are scattered along PCII. An examination of the higher numbered principal components indicates that they contribute little to understanding differences in the P_4 shapes. Plots of individuals along these components show complete intermixing of the data points.

Discriminant functions

To test how well the P_4 shape separates Neandertals from amHs and other fossil hominids I ran a four-group discriminant functions analysis. Discrimination is based on calculating Mahalanobis distances of individuals to group centers and then allocating each individual to the group to which it is closest. For this analysis all amHs (contemporary and fossil) were combined into one group since the primary question is how well P_4 shape discriminates between Neandertals and amHs samples.

Table 5.33 presents the results of the discriminant functions analysis. Using 29 variables the best linear discriminant function misclassifies 16 out of 136 crown shapes, making the average a posteriori error rate of this classification 11.8%. Of the four groups amHs has the highest rate of correct classification. In this case, four out of the 106 crown shapes were misclassified, giving an error rate of only 3.8%. Of the four misclassified amHs P_4 crowns two were misclassified as Neandertal, and two were misclassified as *Homo erectus*. Of the two amHs that were misclassified as a Neandertal, one was from the Upper Paleolithic amHs sample (Dolní Věstonice) and the other was from the contemporary amHs sample (India). Both of these individuals possess a P_4 with a

reduced lingual cusp relative to its buccal cusp and/or an asymmetrical contour. Of the two amHs that were misclassified as *Homo erectus*, one was from the early amHs sample (Qafzeh 7) and one was from the contemporary amHs sample (China). These two specimens are similar in the relative size (wider) and the shape (square) of their lingual cusp.

The error rate of the classification for Neandertals was quite a bit higher than that found for the amHs. Here, seven of the 20 Neandertal P_4s were misclassified, resulting in an error rate of 35%. Six of these were misclassified as amHs while one was misclassified as *Homo erectus*. Although this is not particularly reassuring, information with regard to shape differences does emerge from this analysis. A visual inspection of the misclassified teeth confirms the general shape differences that this analysis captures. Misclassified Neandertals possess wider lingual cusps and are more symmetrically shaped than the correctly classified teeth. Five of the Neandertal P_4s that were misclassified as amHs were from the Krapina sample. These five represent approximately 42% of the total Krapina sample (n = 12). Clearly the Krapina sample, which includes some of most (D50) and least (D30) asymmetrical teeth, is highly variable with regard to P_4 shape.

The a posteriori error rate for the remaining two groups was similar to (archaic Hs) or worse than (*Homo erectus*) that found for Neandertals. This is not surprising, considering the small sample sizes. The most interesting results from this portion of the analysis come from inspecting the cases that were misclassified. Here one of the three archaic *Homo sapiens* teeth (Mauer) was misclassified as a Neandertal. In the case of the

Homo erectus teeth four of the eight were misclassified as amHs (two from Ternigif, one from KNM-WT15000 and one from KNM-ER 992 – all African *Homo erectus* spanning approximately 1.0 million years). While it is tempting to conclude from these results that archaic *Homo sapiens* P_4s are more like those of Neandertals than other fossil human groups, the small sample size (n = 3) requires cautious interpretation.

TABLE 5.33 Classification of P_4s using discriminant functions

	Percent correct	Archaic *Homo sapiens*	*Homo erectus*	amHs	Neandertal
Archaic *Homo sapiens*.	66.7	2	0	0	1
Homo erectus	50.0	0	4	4	0
amHs (pooled)	96.2	0	2	101	2
Neandertal	**65.0**	**0**	**1**	**6**	**13**

* Rows represent how individuals were classified/misclassified.

Summary of P_4 morphometrics

This analysis of the occlusal crown contour of P_4 indicates that significant differences exist between amHs and Neandertals. Although the analysis of mean shape suggested that this difference is attributable to an asymmetrical crown contour in Neandertals, the PCA of the Elliptic Fourier coefficients indicates that the relative width of the lingual cusp may contribute as well. This is not surprising, as the relative size of the lingual cusp is partially a byproduct of the tooth crown asymmetry. In asymmetrical

teeth the mesial lingual lobe appears to be truncated, contributing to a smaller lingual cusp area.

The discriminant functions analysis showed that the Neandertal and amHs P_4 can be separated based on shape alone. However, while the correct classification for amHs was very good (97% correct) the classification for Neandertals was not as good (65% correct). Better discriminatory power between Neandertals and amHs has been obtained using mandibular molar enamel thickness (Zilberman and Smith, 1992). Nonetheless, compared with other measurements of P_4 shape or size (e.g., crown index) the tooth crown contour does produce better discrimination.

From the point of view of assigning unknown specimens to taxonomic groups it is unlikely than an amHs P_4 will be misclassified as a Neandertal based on the P_4 outline. However, a Neandertal P_4 has a 35% chance of being misclassified as an amHs based on its outline. Although there is a strong tendency for Neandertal P_4 to be asymmetrical and to have a mesiodistally narrow lingual cusp relative to the buccal cusp, variation in the sample overlaps with that of amHs. However, when the P_4 outline is used in conjunction with the P_4 characters described in the morphology section, there is a low likelihood of misidentifying a Neandertal P_4 as an anatomically modern human.

Discussion of morphological and morphometric analysis

This analysis of morphological and morphometric characters in the Neandertal postcanine dentition has shown that there are some marked differences between Neandertal and contemporary amHs teeth. The major morphological distinction of Neandertal postcanine teeth is the complexity of their occlusal surfaces, which is

characterized by the possession of extra tubercles, crests and fissures. Metrically, Neandertals are distinctive in their possession of buccolingually skewed maxillary molars with internally compressed cusps, and asymmetrical P_4s. Neandertals share some of these features with other fossil hominids but others appear to be unique to them.

Marked morphological differences relating to occlusal complexity are present in the maxillary premolars of fossil and contemporary humans; however, they were not found to be particularly useful for discriminating between Neandertals and other fossil samples. Likewise, Neandertal maxillary molars possess a relatively large hypocone compared to contemporary amHs, but this feature is less useful in separating Neandertals from other fossil hominids. The mandibular dentition appears to be better for discriminating between Neandertals and other human groups. In this case, mandibular second premolars show unique morphology (mesially placed metaconid, multiple lingual tubercles and transverse crest), the combination of which is not found in any other human group. Moreover, the morphometric analysis indicates that the asymmetry observed in Neandertal P_4s is a useful character for discriminating between Neandertals and other human groups. Finally, the mandibular molars appear to possess morphological (but not morphometric) characters that separate Neandertals from other human groups. The major distinctive feature is the presence of a well developed mid-trigonid crest.

Up until now the major distinctions between Neandertal and amHs dental morphology has been the marked prominence of distinctive incisor morphology and taurodont lower molars (Crummett, 1994; Gorjanovič-Kramberger, 1904; Keith, 1913; Patte, 1959; Trinkaus, 1983). Metrically, the major distinctions have been their

exceptionally large buccolingual incisor diameters, their large M_2 compared to M_1 and relatively long M_2 roots compared to those of M_1 (Brace, 1967; Bytnar et al., 1994; Smith, 1989; Trinkaus, 1978b; Wolpoff, 1971). This analysis has shown that, in fact, Neandertals are characterized by a suite of dental traits and dental trait frequencies that have been largely overlooked in the literature. Based on these traits, Neandertals can be identified through their possession of a unique dental pattern that, significantly, is unlike any observed in contemporary amHs. Clearly, a number of these previously unidentified and/or unquantified characters have value both for increasing the database of dental traits (and thus group affinity) and in shedding light on the phylogenetic relationship between Neandertals and amHs.

Introduction

The nature of the relationship between Neandertals and amHs is still at issue even after decades of scientific debate. Relative to the attention afforded to cranial and postcranial morphology, dental morphology has been overlooked as a means to tackle this problem. Dental morphology has a strong genetic component; and, because teeth preserve well over time, relatively large samples of Neandertal and other fossil hominid teeth are available for study. These characteristics make dental morphology a potentially useful tool for understanding the relationships between Neandertals and amHs.

Two approaches are used to investigate the relationships between Neandertals and fossil and recent humans: phenetic and cladistic. The phenetic approach provides an assessment of Neandertal affinity by means of estimating overall similarity from dental trait frequencies. Because all characters are weighted equally (i.e., there is no distinction between primitive and derived states) the phenetic approach makes no assumptions that branching patterns based on similarity/dissimilarity reflect ancestral-descendant relationships. Phenetic dendrograms depict clusters of OTUs that are grouped according to their degree of similarity, with all variables contributing equally to the results. By contrast, the cladistic approach does not weight characters equally. With this method, cladograms are based on sets of shared derived characters. The goal of this cladistic analysis is to examine the distribution of polarized dental character states across fossil and recent human groups. The dental trait frequencies were transformed into discrete character states using the gap weighted method (described below). Polarization of

characters states was accomplished using the outgroup method. The outgroup is considered to exhibit the ancestral character state for the traits under consideration. Character states that differ from the outgroup (ancestral condition) are considered to be derived.

Although cladistic analysis has become a popular tool for understanding evolutionary relationships, it has been pointed out that interpreting the results of cladistic analyses can be problematic – especially at lower (species and below) taxonomic levels (e.g., Crandall et al., 1994; Harrison, 1993; Trinkaus, 1992). A key issue is the potential to violate a number of assumptions inherent to cladistic analysis. For example, studying the morphology of closely related species inevitably involves the problem of homoplasy. In order to interpret cladograms the rule of maximum parsimony is often applied. This method assumes that the majority of characters shared among OTUs have been inherited from a common ancestor (homology) rather than evolved independently (homoplasy). However, evolution at the species level (and especially at the subspecies level) is complicated by relatively high levels of homoplasy. The similarity of genomes (as in most of the samples used in this study) and the potential for interbreeding leads to the expectation that homoplasy will be high.

Other issues have been outlined by Trinkaus (1992). These include determining the units of analysis, identifying which characters to use and predicting character polarity (rooting a tree). Some of these problems can be avoided by using dental morphology. For example, because taxonomic identification of Middle-Upper Pleistocene hominids has been primarily based on cranial and postcranial remains, dental morphology provides

an independent source of information and avoids (to some extent) the problem of tautology. As to choosing characters for analysis, most dental morphological traits are only minimally intercorrelated (Scott and Turner, 1997). In this respect, they are potentially good characters for cladistic analysis.

The primary problem with dental traits is the fact that they often exhibit continuous ranges of variation. To solve this problem the gap weighting method (Thiele, 1993) is employed to transform continuous trait frequencies into discrete character states. This method assigns character states based on the rank order of the trait frequency and the naturally occurring gaps between trait frequencies. Gaps are differentially weighted according to their size (larger gaps are weighted more heavily than smaller gaps).

Other problems are harder to avoid, including those issues such as anagenic population divergence and hybridization or reticulation among the groups being studied. These issues notwithstanding, applying this approach allows the work to be placed in a historical context and provides a working phylogenetic hypothesis against which the dental morphological data can be tested.

Phenetic analysis

Objective

The goal of the phenetic analysis is to determine which samples show the greatest similarity to Neandertals in the size and morphology of the postcanine dentition. If amHs evolved as the result of gradual *in situ* evolution (or extensive admixture with local archaic populations) it is hypothesized that Neandertals should be (dentally) more similar

to early amHs from the same geographic region than they are to amHs from other geographic regions.

Analyses

The phenetic analysis consists of assessments of biological affinity and cluster analyses. I used the multivariate Mean Measure of Divergence (MMD) statistic to assess biological affinity (Smith in Berry and Berry [1967]), with the Green and Suchey (1976) correction method for small samples size. This method provides a measure of phenetic similarity based on the entire suite of dental traits. Divergence between two samples was considered significant at the .025 level of probability when the MMD is greater than twice the standard deviation (Sjøvold, 1973).

Cluster analyses were based on dissimilarity matrices derived from MMD values. Ward's Method is the clustering algorithm generally preferred by dental anthropologists because it has been shown that the clusters produced conform to known population relationships based on other (e.g., genetic) data. This method bases cluster membership on the total sum of squared deviations from the mean of the cluster. The criteria for grouping is that it should produce the smallest possible increase in the error sum of squares (Ward, 1963).

Small sample sizes in some of the fossil hominid samples precluded using all 26-traits in every pair-wise comparison. In fact, there were only 12 traits for which all groups had a sample size of three or more individuals. For this reason, the phenetic analysis was broken up into three parts, each with a different objective.

The goal of the first analysis was to determine to which sample the Neandertal sample is most phenetically similar. Multiregional evolution predicts that geographic areas will show inter-regional differences that persist over time. A reasonable hypothesis, therefore, would be that archaic populations in one geographic region (in this case Europe) will show closest phenetic affinity to recent populations in the same geographic region. To test this hypothesis the early and late Neandertals were pooled and pair-wise comparisons were then made between the pooled Neandertal sample and contemporary amHs samples. Pooling the early and late Neandertal samples provided a sample size that was comparable to that of the contemporary amHs groups; it also made it possible to use all 26 dental traits in the analysis (see Table 6.1).

The second analysis adds additional hominid samples to assess the phenetic affinities of these and recent human samples. For all samples to be compared equally (using the same number of traits), only 12 dental traits could be used (see Table 6.1). As above, the MRE hypothesis predicts that archaic populations (e.g., Neandertals) will be more similar to their contemporary amHs geographic counterparts.

The third analysis examines temporal change in Europe. In this analysis, the Neandertal sample is split into earlier and later groups to assess changes (if any) over time. The same set of 12 dental traits used in the second analysis are used in the third analysis. If modern Europeans evolved through gradual evolution in Europe, one may expect MMD values to decrease between earlier and later European populations. In addition, if there was significant gene flow between late Neandertal and Upper Paleolithic amHs populations we may expect this to be apparent from the MMD values.

TABLE 6.1. Traits used in different phenetic analyses

26 Trait Analysis	*12 Trait Analysis*
P^4 Buccal MaxPAR	M^2 Hypocone
P^4 Lingual MaxPAR	P_3 Lingual cusps
P^4 Accessory cusps	P_3 Transverse crest
M^1 Cusp 5	P_4 Metaconid placement
M^1 Carabelli's Cusp	P_4 Transverse crest
M^2 Hypocone	P_4 Asymmetry
P_3 Lingual cusps	M_1 Distal trigonid crest
P_3 Transverse crest	M_1 Mid-trigonid crest
P_3 Asymmetry	M_1 Cusp 7
P_3 Distal accessory ridge	M_1 Anterior fovea
P_3 Mesial accessory ridge	M_2 Y groove pattern
P_3 Mesial lingual groove	M_2 Four cusped molar
P_4 Metaconid placement	
P_4 Lingual cusps	
P_4 Transverse crest	
P_4 Asymmetry	
P_4 Distal accessory ridge	
P_4 Mesial accessory ridge	
M_1 Deflecting wrinkle	
M_1 Distal trigonid crest	
M_1 Mid-trigonid crest	
M_1 Cusp 6	
M_1 Cusp 7	
M_1 Anterior fovea	
M_2 Y groove pattern	
M_2 Four cusped molar	

Results

In the first analysis, all pair-wise comparisons between Neandertal and contemporary amHs show high and significant MMD values (Table 6.2). In fact, based on these very high numbers, it would be inaccurate to claim that Neandertals were phenetically similar to any contemporary amHs group. Based on 26 postcanine dental traits, Neandertals are *least dissimilar* to the Australian sample (MMD = 0.756), followed by the Near East (MMD = 0.793) sample. They are most divergent from the Indian sample (MMD = 1.336), followed by the European sample (MMD = 1.159). The results of this analysis do not suggest a greater phenetic similarity between Neandertals and contemporary Europeans, as may be expected if geographic dental differences have deep historical roots. In fact, quite the opposite is true: the European sample is one of the least similar to the Neandertal sample.

To clarify the significance of these distances, it is useful to compare these MMD values with those found among contemporary human samples (see Table 6.2). Among contemporary amHs the highest MMD obtained for any pair-wise comparison is found between the Australian and Indian samples (MMD = 0.471). These represent the most complex and most simplified dentitions (respectively) of all the contemporary amHs samples. Still, this MMD is less than half that obtained for four of the seven Neandertal –contemporary amHs comparisons, with the remaining Neandertal–contemporary amHs comparisons resulting in MMDs nearly one and one half times this value. Hence, the Neandertal postcanine dental morphology is more divergent from all contemporary amHs than are the most divergent contemporary amHs groups from one another.

TABLE 6.2. Results of the 26-trait MMD analysis for all groups[1,2]

Neandertal	North Africa	West Africa
0.756* Australasia	0.000 Near East	0.050 Australasia
0.793* Near East	0.109* Europe	0.060 Near East
0.896* North Africa	0.130* Northeast Asia	0.125* North Africa
0.925* West Africa	0.113* India	0.134* Northeast Asia
1.083* Northeast Asia	0.125* West Africa	0.239* Europe
1.159* Europe	0.206 Australasia	0.348* India
1.336* India	0.896* Neandertal	0.793* Neandertal
Asia	**India**	**Near East**
0.114 Australasia	0.005 Europe	0.000 North Africa
0.089* Europe	0.113* North Africa	0.036 Europe
0.090* Near East	0.114* Australasia	0.060 West Africa
0.130* North Africa	0.138* Near East	0.090* Northeast Asia
0.134* West Africa	0.140* Northeast Asia	0.116* Australasia
0.140* India	0.348* West Africa	0.138* India
1.083* Neandertals	1.336* Neandertals	0.793* Neandertals
Europe	**Australasia**	
0.036 Near East	0.050 West Africa	
0.046 India	0.114* Northeast Asia	
0.089* Northeast Asia	0.116* Near East	
0.109* North Africa	0.199* Europe	
0.199* Australasia	0.206* North Africa	
0.239* West Africa	0.471* India	
1.159* Neandertals	0.756* Neandertals	

[1] An asterisk (*) denotes statistically significant (α =.025)
[2] Postcanine traits only.

A cluster analysis of the MMD values illustrates just how divergent Neandertal postcanine dentition is from that of contemporary amHs (Fig. 6.1). Here the linkage distance between the Neandertal sample and the contemporary amHs cluster is nearly four times (~1.65) that of the distance between the next two clusters (~ 0.45). The Neandertal sample does not show affinity to any contemporary human group and, in fact, is an outlier among the samples. That this dendrogram is an accurate measure of divergence (at least among contemporary amHs) is supported by the fact that the amHs relationships found here are in general agreement with those of other researchers (Scott and Turner, 1997; Turner, 1992a).

The second analysis examines the phenetic distances of fossil and contemporary human groups. As noted, due to small sample sizes only 12 traits were used in this analysis. The consequence of reducing the number of characters was to increase the magnitude of MMD values overall. However, the pattern of similarity differs little from the pattern obtained using 26 traits.

The MMD values for the 12-trait comparisons are presented in Table 6.3. Based on this analysis Neandertals show significantly high MMD values for comparisons with all but the archaic *Homo sapiens* group, from which they are indistinguishable (MMD = 0.000). Among the fossil hominids, Neandertals are most similar to early amHs and most dissimilar to Upper Paleolithic amHs. The early amHs sample is equidistant and indistinguishable from both Upper Paleolithic and *Homo erectus* samples.

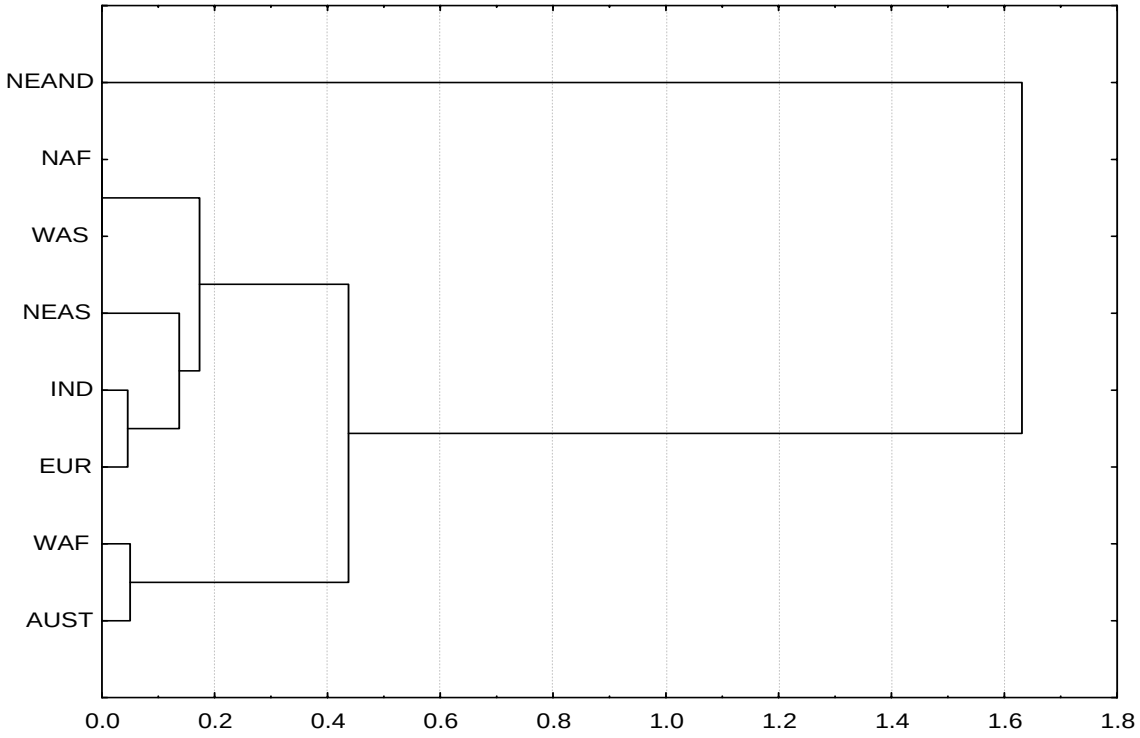


Fig. 6.1. Dendrogram produced from MMD values for Neandertals and contemporary human samples. Ward's method 26 dental traits. (NEAND: Neandertal; NAF: North Africa; WAS: Near East; NEAS: Northeast Asia; IND: India; EUR: Europe; WAF: West Africa; AUST: Australia).

The *Homo erectus* and Upper Paleolithic samples, on the other hand, show moderate and significantly different MMD values (MMD = 0.158). Of the fossil samples, the early amHs sample is much more similar to all contemporary amHs samples than is the Neandertal sample. The Upper Paleolithic sample shows the greatest similarity to all contemporary amHs samples.

Of note is the fact that the European Upper Paleolithic sample is not dentally most similar to the contemporary European sample as may be expected if they contributed significantly to their evolutionary history. Instead, this sample is closest to the Asian (MMD = 0.047) and Australian samples (MMD = 0.060) using 12 dental traits; and to the Near Eastern (MMD = 0.082) and North African samples (MMD = 0.076) using 19 dental traits. I will return to this point at the end of the chapter.

A cluster analysis based on 12-trait MMD values is presented in Fig. 6.2. Here, there are two main clusters: (1) The Neandertal and archaic *Homo sapiens* samples and (2) all other samples. The linkage distance separating the first two clusters is very high (3.4) compared to the linkage distance separating the third and fourth clusters (0.70). Within the second cluster there are two main clusters: (3) one that links Upper Paleolithic and early amHs samples with West African, Australian and Asian samples and (4) one that links North African/Near Eastern with European/Indian samples. With the exception of the Asian sample (which now links with West Africa and Australia), the same contemporary amHs clusters are found in this 12 trait analysis as are found in the larger 26 trait analysis (Fig 6.1).

TABLE 6.3. Results of the 12-trait MMD analysis for all groups[1,2]

Homo erectus	Archaic *Homo sapiens*	Neandertal
0.000 Early amHs	0.000 Neandertals	0.000 Archaic *H. sapiens*
0.011 Archaic *H. sapiens*	0.011 *Homo erectus*	0.395* *Homo erectus*
0.158* U.P. amHs	0.015 Early amHs	0.653* Early amHs
0.322* West Africa	0.324* U.P. amHs	1.159* U.P. amHs
0.395* Neandertals	0.517* Australasia	1.362* Australasia
0.399* Australasia	0.706* Near East	1.537* Near East
0.403* Northeast Asia	0.848* North Africa	1.661* North Africa
0.567* North Africa	0.989* Europe	1.679* West Africa
0.730* Near East	0.716* West Africa	1.654* Northeast Asia
0.858* Europe	0.689* Northeast Asia	1.954* Europe
0.902* India	1.144* India	1.996* India
Early modern humans	Upper Paleolithic amHs	North Africa
0.000 *Homo erectus*	0.000 Early amHs	0.016 Near East
0.000 U.P. amHs	0.046 Northeast Asia	0.051 Australasia
0.015 Archaic *H. sapiens*	0.060 Australasia	0.076 Europe
0.148* Australasia	0.121* North Africa	0.121* U.P. amHs
0.243* Northeast Asia	0.158* *Homo erectus*	0.132* Northeast Asia
0.322* North Africa	0.182* West Africa	0.158* India
0.335* West Africa	0.185* Europe	0.163* West Africa
0.388* Europe	0.187* Near East	0.322* Early amHs
0.423* India	0.324* Archaic *H. sapiens*	0.639* *Homo erectus*
0.449* Near East	0.352* India	0.848* Archaic *H. sapiens*
0.653* Neandertals	1.159* Neandertals	1.661* Neandertals
West Africa	Asia	India
0.053 Australasia	0.007 Australasia	0.005 Europe
0.099 Northeast Asia	0.017 Near East	0.137* Near East
0.163* North Africa	0.046 U.P. amHs	0.158* North Africa
0.182* U.P. amHs	0.099 West Africa	0.223* Northeast Asia
0.227* Near East	0.132* North Africa	0.352* U.P. amHs
0.270* Europe	0.118* Europe	0.383* West Africa
0.322* *Homo erectus*	0.223* India	0.423* Early amHs
0.335* Early amHs	0.243* Early amHs	0.432* Australasia
0.383* India	0.403* *Homo erectus*	0.902* *Homo erectus*
0.716* Archaic *H. sapiens*	0.689* Archaic *H. sapiens*	1.144* Archaic *H. sapiens*
1.537* Neandertals	1.654* Late Neandertals	1.996* Neandertals

TABLE 6.3 (continued)

Near East	Europe	Australasia
0.010 Europe	0.005 India	0.051 North Africa
0.016 North Africa	0.010 Near East	0.053 West Africa
0.017 Northeast Asia	0.076 North Africa	0.060 U.P. amHs
0.093 Australasia	0.086* Australasia	0.086* Europe
0.137* India	0.118* Northeast Asia	0.093 Northeast Asia
0.187* U.P. amHs	0.185* U.P. amHs	0.148* Early amHs
0.227* West Africa	0.270* West Africa	0.227* Near East
0.449* Early amHs	0.388* Early amHs	0.399* *Homo erectus*
0.706* Archaic *H. sapiens*	0.858* *Homo erectus*	0.432* India
0.753* *Homo erectus*	0.989* Archaic *H. sapiens*	0.517* Archaic *H. sapiens*
1.537* Neandertals	1.954* Neandertals	1.362* Neandertals

[1] An asterisk (*) denotes statistically significant (α =.025)
[2] Postcanine traits only.

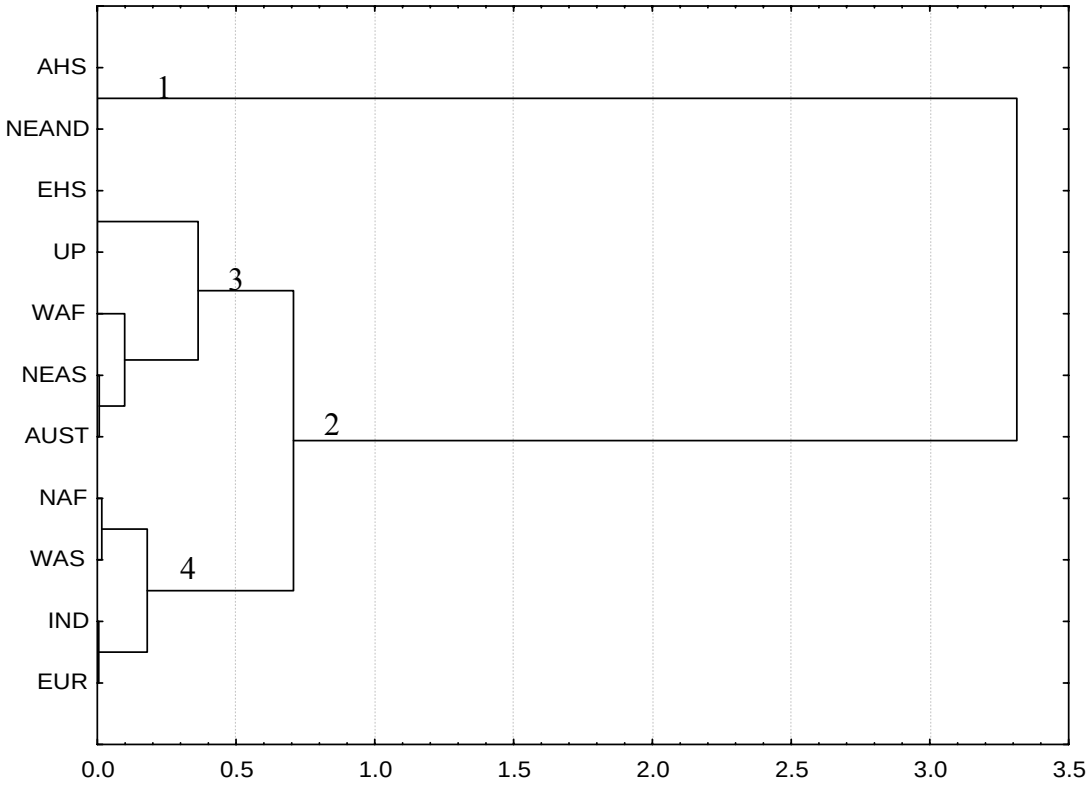


Fig. 6.2 Dendrogram produced from MMD values for Neandertals and contemporary human samples. Ward's method using12 dental traits. (AHS: Archaic *Homo sapiens;* ENEA: Early Neandertal; LNEA: Late Neandertal EHS: Early amHs; UP: Upper Paleolithic; NAF: North Africa; WAS: Near East; NEAS: Northeast Asia; IND: India; EUR: Europe; WAF: West Africa; AUST: Australia

The third analysis examines dental morphological change over time by comparing the MMD values of European archaic *Homo sapiens*, Neandertal, Upper Paleolithic amHs and contemporary samples. In this analysis the Neandertal sample is broken up into earlier and later samples to identify any trends in the data. The results (based on 12 dental traits) are presented in Table 6.4. For comparison, the MMD values between European samples and early amHs and *Homo erectus* are also presented.

Of the fossil hominid samples, the Upper Paleolithic Europeans show the closest affinity (MMD = 0.185) to the contemporary European sample while the early and late Neandertal samples are the least like the contemporary European sample (MMD = 1.715 and 1.962, respectively). Although even older chronologically, the archaic *Homo sapiens* sample is phenetically closer to the contemporary European sample than are either of the Neandertal samples (MMD = 0.989). Interestingly, even the early amHs and *Homo erectus* samples are dentally more similar to Upper Paleolithic (MMD = 0.000 and 0.158, respectively) and contemporary Europeans (MMD = 0.388 and 0.858, respectively) than are either of the Neandertal samples.

A comparison of the earlier and late Neandertal samples with the contemporary European and Upper Paleolithic amHs sample shows that the MMD values are high and significant (Table 6.4). The late Neandertal sample does show slightly lower MMD values for the Upper Paleolithic and contemporary European comparisons than the early Neandertals. However, this difference is not easily interpretable. Late Neandertals are more like *all* contemporary amHs groups than early Neandertals (see Table 6.5) and do not show a particular trend towards the European dental pattern. Moreover, the MMD

TABLE 6.4. Results of the12-trait MMD analysis for European samples with Early amHs and Homo erectus added for comparison[1,2]

Contemporary Europe	Upper Paleolithic Europe	Archaic *Homo sapiens*
0.185* U.P. amHs	0.185* Europe	0.000 Early Neandertal
0.989* archaic *H. sapiens*	0.324* archaic *Homo sapiens*	0.000 Late Neandertal
1.715* Late Neandertal	0.996* Late Neandertal	0.324* U.P. amHs
1.962* Early Neandertal	1.176* Early Neandertal	0.989* Europe
0.388* Early amHs	0.000 Early amHs	0.015 Early amHs
0.858* *Homo erectus*	0.158 *Homo erectus*	0.011 *Homo erectus*

Late Neandertal	Early Neandertal
0.000 Early Neandertal	0.000 Late Neandertal
0.000 archaic *Homo sapiens*	0.000 archaic *Homo sapiens*
0.996* U.P. amHs	1.176* U.P. amHs
1.715* European	1.962* Europe
0.570* Early amHs	0.672* Early amHs
0.349* *Homo erectus*	0.416* *Homo erectus*

[1] An asterisk (*) denotes statistically significant (α =.025).
[2] Postcanine traits only.

TABLE 6.5 Early and late Neandertal MMD comparisons with Upper Paleolithic and contemporary human samples based on 12 traits[1,2]

	Early Neandertal	Late Neandertal
Upper Paleolithic amHs	1.176	0.996
Australasia	1.357	1.192
Near East	1.565	1.301
Northeast Asia	1.267	1.249
North Africa	1.632	1.489
West Africa	1.446	1.259
Europe	1.962	1.715
India	1.995	1.774

[1]All MMD values are significant.
[2] Postcanine traits only.

values for the Upper Paleolithic and contemporary amHs – late Neandertal comparisons remain very high and significant. They are, in fact, higher than the largest MMD value found between two contemporary populations living in widely separated geographic areas (see Table 6.1). Although consistent with the MRE prediction that late Neandertals will be more like Upper Paleolithic and contemporary Europeans than early Neandertals, this evidence is far less compelling than the very large and significant MMD values retained in the late Neandertals sample.

Discussion of phenetic results

The results of this phenetic analysis are in general agreement with those of earlier studies based on a different set of tooth traits and different sample composition (Bailey, 2000a; Bailey and Turner, 1999). This indicates that with certain exceptions (e.g.,

Northeast Asian populations, see discussion below) postcanine dental morphology alone has similar discriminatory power to that of a combined anterior/posterior dental trait set.

Assuming that MMDs accurately reflect biological distances among populations, the results obtained from this phenetic analysis are not consistent with the expectations of MRE. Neandertals are not more similar to either earlier (Upper Paleolithic) or later (contemporary) European samples than they are to other amHs samples. In addition, Neandertal dental morphology is not intermediate between *Homo erectus* and Upper Paleolithic or contemporary Europeans, as MRE might predict. Assuming that *Homo erectus* represents the primitive condition, there is evidence of gradual evolution towards the recent European dental pattern through early amHs and Upper Paleolithic amHs *only if Neandertals are not included in the temporal sequence*. The Neandertal sample produces a significant disruption in the gradual evolution of the modern pattern. Finally, the analysis indicates that recent Europeans are dentally more similar to early amHs than they are to archaic humans in their own region (archaic *Homo sapiens* and Neandertals), as would be predicted by the RAO model.

An alternative interpretation to the above evidence has been suggested by Relethford in recent papers. In these papers, Relethford proposes that the same pattern of biological distance that is taken here to support a replacement event (RAO) would also be predicted from a gene flow and migration model if the long term population size of Africa was larger than that of other regions (Harpending and Relethford, 1997; 2001a; Relethford and Jorde, 1999b). He argues that if gene flow was primarily in one direction (out of Africa) and if the emigrant amHs populations were numerically larger, they would

eventually "swamp" the Neandertals genetically. Thus, because more of their ancestry comes out of Africa than from the Neandertals, recent and living Europeans would, over time, be expected to look more like early amHs than they look like Neandertals (Relethford, personal communication, 2002). However, while this *could* explain why most traits do not show continuity, it is still expected that some will. Unlike Wolpoff (Wolpoff et al., 2000) and Frayer (1992) who have found low frequencies of Neandertal traits in Upper Paleolithic Europeans, none of the regional Neandertal dental characters that I have identified appear to show up in Upper Paleolithic Europeans. Any dental characters that show continuity between Upper Paleolithic Europeans and Neandertals are also present in *Homo erectus*, and so are likely primitive in nature.

The finding that the archaic *Homo sapiens* sample is dentally more similar to the Neandertal samples (early and late, MMD = 0.000) than to the early amHs or *Homo erectus* samples (MMD = 0.015 and 0.011, respectively) may be significant in light of recent hypotheses positing that European archaic *Homo sapiens/H. heidelbergensis* gave rise exclusively to Neandertals (Rosas and Bermúdez de Castro, 1998). Even so, the MMD comparisons between the archaic *Homo sapiens* sample and the early amHs and *Homo erectus* sample are not particularly high nor statistically significant. Considering this together with the small number of individuals in the archaic *Homo sapiens* and early amHs samples, these phenetic results (which are consistent with the hypothesis of a unique archaic *Homo sapiens*-Neandertal evolutionary relationship) should be interpreted cautiously.

The finding that the Upper Paleolithic European sample is not more similar to the contemporary European sample warrants further discussion here. The results can be interpreted in a number of ways, some of which follow. First, it is possible that the small number of postcanine dental traits used in this particular MMD analysis gives an incomplete signal of biological distance. Adding anterior dental traits to the analysis would undoubtedly change the pattern of the observed relationships. For example, Northeast Asians are highly derived in their anterior dental morphology (Turner, 1990a), while Upper Paleolithic Europeans are not (Bailey, unpublished data). Therefore, the low MMD value (0.046) found between these two samples would certainly be much higher if anterior dental traits were added. On the other hand, results of an earlier study that combined 18 anterior and posterior dental traits confirms the close biological relationship between Upper Paleolithic Europeans and early amHs indicated here, while at the same time indicating a much closer relationship between Upper Paleolithic and recent European samples than found here (Bailey, 2000a). Therefore, while adding traits to the analysis would change some of the relationships observed, others would most likely not be affected.

Second, it is possible that the Upper Paleolithic sample is, in fact, representative of the ancient European stock, but that this group had not yet differentiated dentally. The Upper Paleolithic sample comprises individuals spanning the Aurignacian and Magdalenian periods – roughly 35,000 to 12,000 years BP. The question is, is this enough time for sufficient microevolution to take place that would account for the observed MMD values? Based on divergence times of several different populations

(Native American, Asian and Pacific islanders) derived from independent archaeological and linguistic evidence, Turner (1986) has suggested that dental microevolution occurs at a relatively constant rate – 0.01 MMD per 1,000 years +/- 30%. If this rate is correct, then we would expect the MMD between Upper Paleolithic and recent Europeans to be somewhere between 0.120 and 0.350. The observed MMD of 0.185 fits well within these estimates. Therefore, while Upper Paleolithic and recent Europeans are somewhat dentally distinct, microevolution alone could account for the divergence between these two samples.

Finally, it is entirely possible that contemporary Europeans have their dental roots elsewhere (Neolithic migrants, for example) – not in Upper Paleolithic European populations. Information from other sources (mtDNA and the Y-chromosome) supports this hypothesis. MtDNA evidence suggests that the European gene pool is made up of ca. 80% Paleolithic and ca. 20% Neolithic ancestry (Richards et al., 1998). Y-chromosome data agree with this, suggesting that the present European population has been strongly influenced by population movements both corresponding to and subsequent to the Neolithic spread of agriculture (Semino et al., 2000). Other studies also suggest a strong Near Eastern (Neolithic) influence (Barbujani and Bertorelle, 2001; Barbujani et al., 1998; Rosser et al., 2000). In all likelihood, the demographic history of Europe is quite complex and has been influenced by major population movements, as well as genetic drift.

Cladistic analysis

Objective

The goal of the cladistic analysis is to ascertain which samples share the greatest derived dental similarity with Neandertals. If Neandertals contributed significantly to the ancestry of amHs it is hypothesized that these groups should emerge as sister groups in a cladistic analysis, indicating descent from a recent common ancestor unique to them.

Analysis

The analysis includes 13 OTUs and 18 characters. The 13 OTUs consist of the eight contemporary amHs samples, together with the early amHs, Upper Paleolithic amHs, early and late Neandertals and archaic *Homo sapiens* samples described in Materials chapter. *Homo erectus* is employed as an outgroup to root the resulting cladograms. It is considered to be an appropriate outgroup because it represents the closest fossil relative to the groups being evaluated. Although some writers regard the African and Asian *Homo erectus* specimens as representing two distinct species (Homo ergaster and Homo erectus, respectively, e.g., Wood, 1994), this is not necessarily the consensus view (see Bräuer and Mbua, 1992; Harrison, 1993; Turner and Chamberlain, 1989). I chose to pool African and Asian *Homo erectus* specimens together for the purposes of this analysis to provide a larger sample with which to compare the other groups.

Of the 18 characters, ten are from the ASUDAS and eight are from the supplemental system. Of these, only three came from the maxillary dentition. The maxillary dentition is represented by fewer variables to begin with. In addition, some

maxillary traits could not be used because wear prevented the determination of trait frequencies in more than one group. As a matter of protocol, if a character's trait frequency was unknown in more than one group I did not use it in the analysis. The traits used in the analysis were limited to those occurring on the key tooth in a particular tooth field. It is assumed that these are subject to less environmental noise than other teeth in the same field (Dahlberg, 1945). Where the key tooth for a particular trait had not yet been established, the tooth containing the most diagnostic information (i.e., that which discriminates best among groups) was used in the analysis. In some groups (especially archaic *Homo sapiens* and *Homo erectus*) sample sizes were very small. If the sample size for a particular trait was less than three it was not considered in the analysis. The programs PAUP™ 3.0 (Phylogenetic Analysis Using Parsimony: Swofford, 1991) and MacClade 4.0 (Maddison and Maddison, 2000) were used to generate and evaluate different cladograms from the dental trait frequencies

Results

The first step in the cladistic analysis was to obtain weighted trait frequencies (as described in the methods section) for each of the 18 characters. The data were then broken up into 10 and 26 (the maximum allowed by PAUP) character states according to the gap weighting method described by Thiele (1993). Character states were ordered, as required by this method. The reason behind dividing the data up into different numbers of characters states (10 vs. 26) derives from Stringer et al. (1997) who found that using a higher number of character states resulted in trees with better resolution (fewer steps) and a higher consistency index (CI). The CI is a measure of how well the characters fit a

particular tree. The higher the number, the better the fit. A low CI tends to indicate a high degree of homoplasy (similarities due to processes other than shared ancestry) present in the cladogram. In this analysis increasing the number of character states did not improve the resolution of the tree or increase the CI. The most parsimonious trees produced using 10 and 26 character states were identical, and the CI was slightly lower (CI=0.51) using 26 states than it was using 10 (CI=0.53). Therefore I report here only on the results of cladograms obtained from analyses using 10 character states.

The exact search produced a single most parsimonious tree that was 307 steps in length (CI=0.53) (Fig. 6.3). In this tree the early amHs sample emerges as the sister group to all other in-group samples, which are united by reduced frequencies of M^2 hypocone, M_2 Y-pattern and M_1 deflecting wrinkle (Table 6.6). Within this clade there are two major subclades: The first consists of early and late Neandertal samples, which group together as the sister to the archaic *Homo sapiens* sample and the second includes Upper Paleolithic and contemporary amHs samples. The character changes responsible for the clustering of the archaic *Homo sapiens*/Neandertal clade are increased frequencies of P_4 transverse crest, M_1 mid-trigonid crest and M_1 anterior fovea and a decreased frequency of the M_1 deflecting wrinkle. The characters responsible for the Upper Paleolithic/contemporary amHs cluster include reduced frequencies of P_4 transverse crest, M_1 mid-trigonid crest, M_2 Y pattern, and M_1 anterior fovea and increased frequencies of 4 cusped M_2, and P_3 distal lingual groove (Table 6.6).

Within the amHs clade the West African and Australian samples group together to the exclusion of the other amHs. The North African, Indian, Near Eastern and European

samples cluster together while the Upper Paleolithic and Northeast Asian samples cluster together. Finally, the European, Indian and Near Eastern samples cluster together with the latter two forming a clade of their own.

To explore the consistency of the OTU grouping in the single most parsimonious tree, all of the trees requiring up to three additional steps were examined. Increasing the tree lengths to 310 steps resulted in 26 trees. PAUP generated two trees of 308 steps, eight trees of 309 steps, and 15 trees of 310 steps. A strict consensus tree used to summarize the 26 alternative trees results in a Neandertal/archaic *Homo sapiens* clade that is preserved in 100% of the trees, although the relationships of the groups within their clade are unresolved (Fig. 6.4). The Upper Paleolithic – contemporary amHs clade is also preserved in the strict consensus tree, although there is little resolution within this group, as would be expected in a tree containing infraspecific groups. The strict consensus of the 11 most parsimonious cladograms is identical to the one found above for 26 trees. However, the strict consensus of the three most parsimonious cladograms resolves the Neandertal-archaic *Homo sapiens* relationship. Here, the three most parsimonious trees place the early and late Neandertals together as a sister group to the archaic *Homo sapiens* sample (Fig. 6.5).

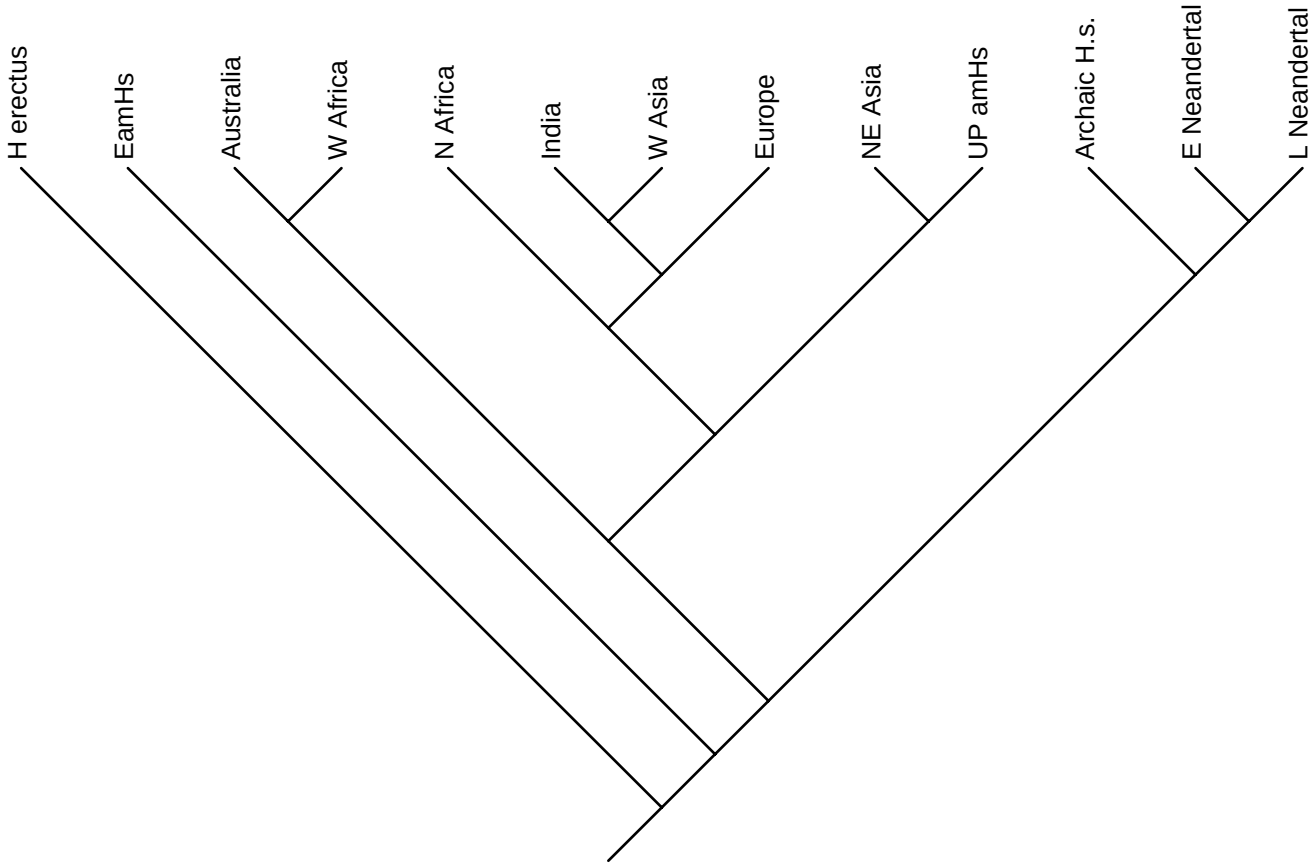


Fig. 6.3. Most parsimonious cladogram generated using 18 characters and 10 character states.

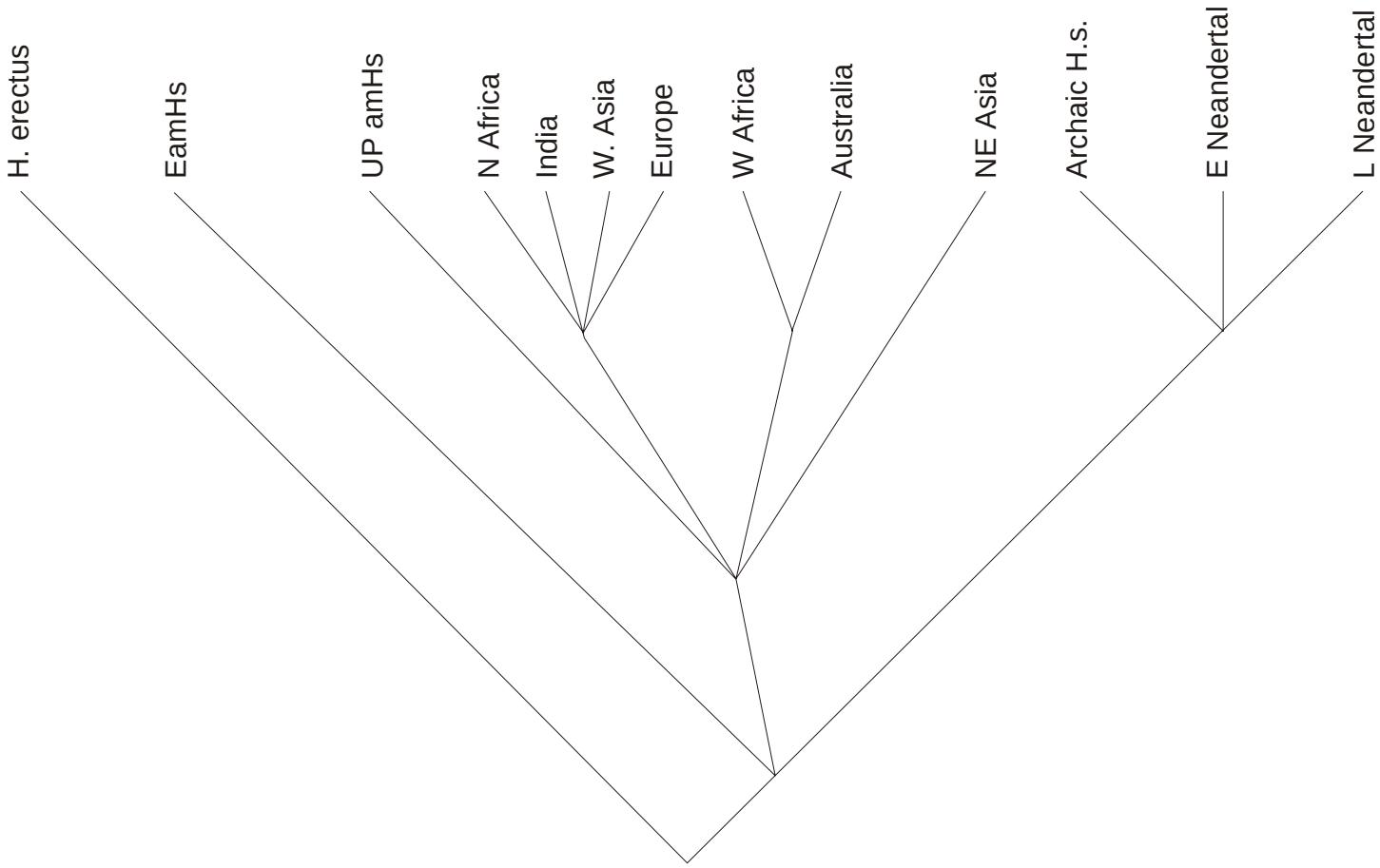


Fig. 6.4. Strict consensus tree of 26 and of 11 most parsimonious cladograms.

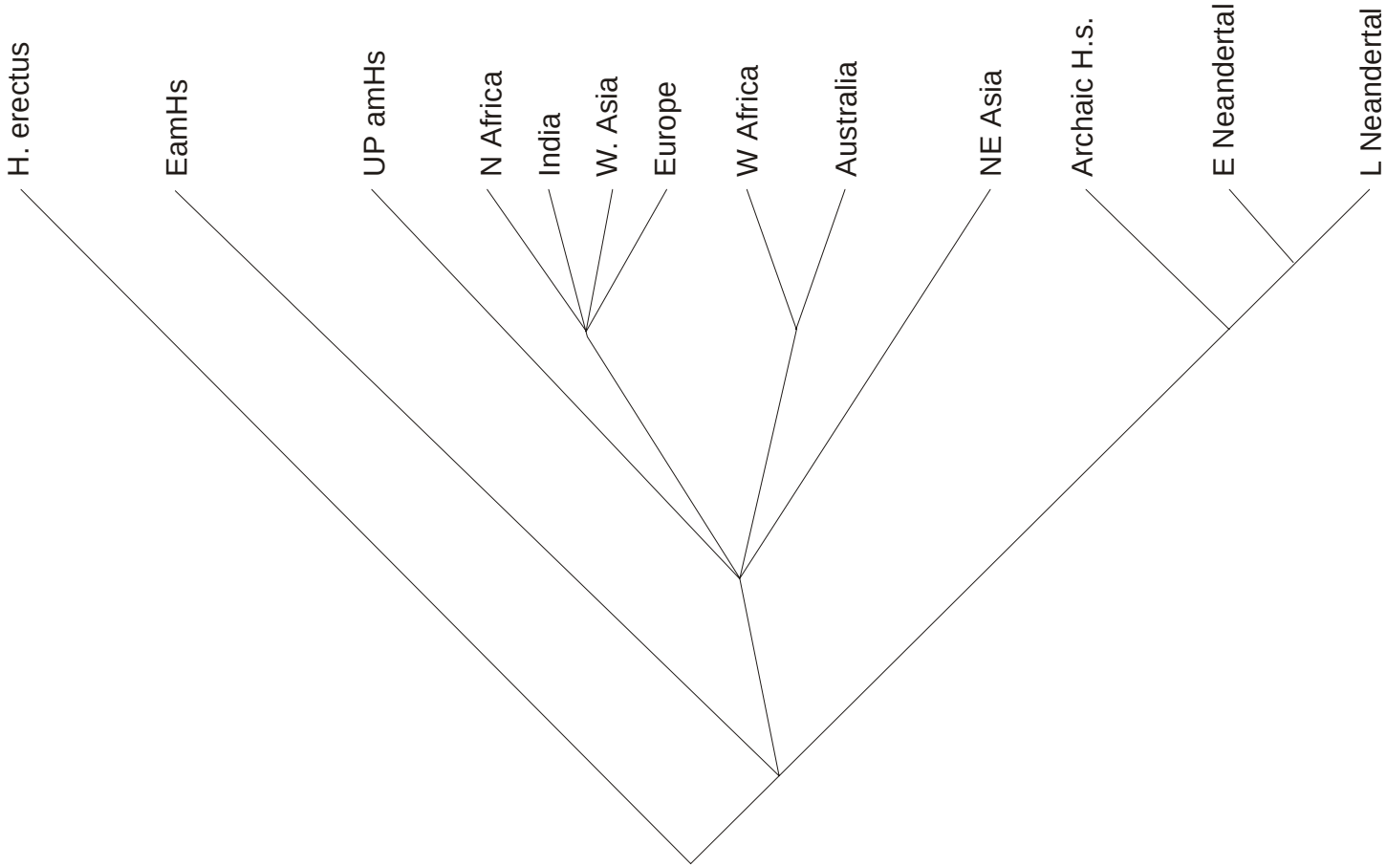


Fig. 6.5. Strict consensus of 3 most parsimonious cladograms.

To get a better idea of the frequency with which particular samples grouped together in each of the trees I used the 75% majority rule to generate consensus trees from the 26, 11 and 3 alternative cladograms. Using the most conservative approach (that based on 26 cladograms), the 75% majority rule tree was identical to the one generated using strict consensus. Using 11 trees, the 75% majority rule preserves the Neandertal-archaic *Homo sapiens* cluster in all 11 trees and the early Neandertal-late Neandertal cluster in 91% (10/11) of the trees (Fig. 6.6). The unresolved polytomy between early amHs, the Neandertal-archaic *Homo sapiens* cluster and the remaining amHs is resolved using the 75% rule. Here in 82% of the cases (9/11), the early amHs sample clusters with the rest of the amHs samples.

Three character states support the clade consisting of early and late Neandertal samples. These include high frequencies (relative to other samples) of P_4 asymmetry (68%-78%), M_1 mid-trigonid crest (84%-94%) and M_1 Cusp 6 (12%-13%). Two of these characters (high frequency of P_4 asymmetry and M_1 mid-trigonid crest) were hypothesized to be unique Neandertal characters based on the phenetic analysis. Thus, these results suggest that the high frequency of P_4 asymmetry and M_1 mid-trigonid crest are likely autapomorphic for Neandertals.

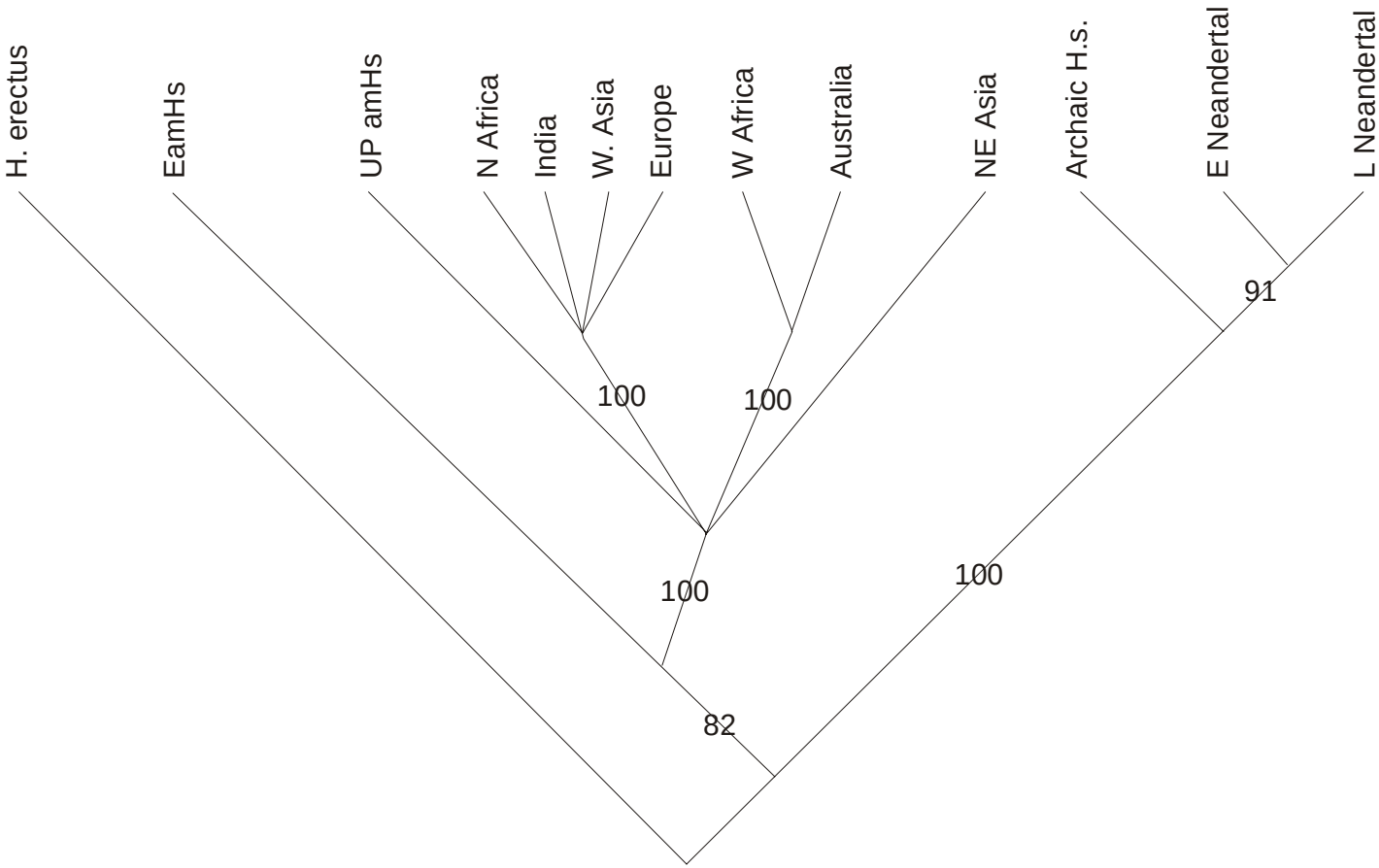


Fig. 6.6. The 75% majority consensus tree produced from the 11 most parsimonious cladograms.

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TABLE 6.6. Character states (expressed as weighted frequencies) that unite samples into clades using the most parsimonious tree

	Low frequency traits	Moderate frequency traits	High frequency traits
Neandertal/amHs clade	Deflecting wrinkle (2: 12%-18%)	Hypocone (4: 69%-72%) M_2 Y Pattern (6: 65%-74%)	
Neandertal/Archaic *Homo sapiens* clade	Deflecting wrinkle (0: 0%-3%)		P_4 transverse crest (7: 62%-69%) M_1 mid-trigonid crest (7/8: 73%-94%) M_1 anterior fovea (7/8/9: 50%-63%)
Contemporary and Upper Paleolithic amHs clade	P_4 transverse crest (1: 9%-17%) M_1 mid trigonid crest (0: 0%-5%) M_2 Y pattern (2: 24%-33%) 4 cusped M_2 (2: 17%-27%) P_3 distal lingual groove (1/2/3: 3%-16%) M_1 anterior fovea (3: 27%-32%)		

Discussion of cladistic results

The rather mediocre consistency index (0.53) obtained in this analysis is not surprising given the large number of characters used, as well as the fact that all character states were ordered (required by the gap weighting method) and could change in only one direction. The CI's obtained suggest that a moderate amount of homoplasy is present in the cladograms. This is not unexpected. Within species reticulation may distort cladograms considerably, and gene flow among the contemporary modern human populations undeniably contributes to the degree of homoplasy found. In addition, the likelihood that the observed similarities are attributable to homoplasy increases when working with groups that are closely related. This is because evolutionary processes working on very similar biological frameworks may result in like morphologies.

The most parsimonious tree found in this study was compared to the most parsimonious tree proposed by Stringer et al. (1997). While both studies deal with dental traits, the character sets employed are considerably different. Stringer et al.'s character set included only nine traits, several of which were anterior tooth traits; this study utilized 18 traits, all of which came from the postcanine dentition. Differences in the OTUs aside, the two studies appear to be in general agreement, although my analysis results in a lower consistency index than Stringer et al.'s (0.512 vs. 0.678). This indicates a greater amount of homoplasy present, which is not surprising given that my analysis includes twice as many characters. My results suggest a closer relationship between West Africa and Australia than with other contemporary amHs, which can also be inferred from Stringer et al's results. The North African-European cluster found by Stringer et al. is

supported here. Finally, Stringer et al. found their Neandertal sample to be quite derived when compared to a hypothetical common (dental) ancestor to all contemporary human groups. That Neandertal postcanine dental morphology is derived relative to amHs is also supported by my analysis.

Overall, the results of this cladistic analysis are inconsistent with the phylogenetic hypothesis that Neandertals and amHs share a recent common ancestor that is unique to them. Instead, the data are consistent with a hypothesis that archaic *Homo sapiens* and Neandertals share a more recent common ancestor with each other then either does with any other group represented in this analysis. This Neandertal/archaic *Homo sapiens* cluster is supported by characters identified as probable synapomorphies in the chapter on Postcanine Dental Morphology and Morphometrics. Although the dates of archaic *Homo sapiens* specimens are somewhat imprecise, most researchers agree that they can be placed within a time frame of 200,000 and 500,000 years BP and/or that they clearly predate the earliest amHs. This supports other claims that the Neandertal clade has deep European roots (e.g., Hublin, 1996).

Summary of Neandertal relationships

The phylogeny obtained through parsimony analysis agrees to a large extent with the divisions obtained through phenetic analysis: it confirms the close evolutionary relationship between Neandertals and archaic *Homo sapiens* and a more distant relationship between these two groups and amHs. Both phenetic and cladistic analyses show the samples emerging in two major clusters: one that includes the archaic *Homo sapiens* -Neandertal samples and another that includes all other humans.

Both cladistic and phenetic analyses also largely agree with regard to the major sub-clusters within the larger contemporary amHs cluster: in one cluster are the North Africa-Europe-Near East-India samples and in the other the West Africa-Australasia samples. They differ, however, in the position of the Northeast Asia sample. In the phenetic analysis the Northeast Asia sample clusters with the West Africa-Australasia cluster, while in the cladistic analysis their relationship with other contemporary amHs is unresolved. While Northeast Asians are known to be quite derived in their anterior dental morphology (Turner, 1983), the phenetic analysis suggests that their postcanine dental morphology is less divergent.

Another difference between the two analyses is in the placement of the Upper Paleolithic and early amHs samples relative to one another. In the phenetic analysis the Upper Paleolithic amHs sample links with the early amHs sample but in the cladistic analysis the Upper Paleolithic amHs sample clusters with the contemporary amHs samples. This suggests that the dental similarities that linked the Upper Paleolithic amHs and early amHs samples in the phenetic analysis may be primitive in nature (assuming that *Homo erectus* represents the primitive condition).

One of the more robust findings of the affinity analysis is the distinct Neandertal – archaic *Homo sapiens* cluster, which is supported by the phenetic analysis and is preserved in 100% of the 26 most parsimonious cladograms. With appropriate caution due to small sample sizes, the phenetic and cladistic analyses of dental morphology presented here point to a unique relationship of archaic *Homo sapiens* to Neandertals.

The general consensus found between the phenetic and cladistic analysis implies that the phenetic tree preserves genuine phylogenetic information concerning the relationship between Neandertals and amHs. It also suggests that the primary structure of the cladogram produced has not been considerably affected by intraspecific gene flow. Certain groupings of contemporary amHs could be influenced by gene flow (the North Africa/Europe/Near East/India group, for example) but it would be difficult to make the same claim for the Australia/West Africa group or the Upper Paleolithic/Northeast Asia group. Considering the large temporal separation between Upper Paleolithic and contemporary amHs, it is unlikely that gene flow is responsible for the placement of the former within the latter's clade.

With the advent of sophisticated techniques for extracting and amplifying ancient DNA, the focus of the "relationship debate" has shifted recently to genetic evidence (Hawkes and Wolpoff, 2001; Ingman et al., 2000; Krings et al., 2000; Krings et al., 1999; Krings et al., 1997; Ovchinnikov et al., 2000; Relethford, 2001a). Although the interpretations of the mtDNA data have not gone unchallenged (see Clark, 1997; Parsons et al., 1997; Strauss, 1999), the results are compelling. Evidence from mtDNA suggests that: 1) the average distance between Neandertal and contemporary amHs genomes is about three times higher than the average distance among contemporary amHs groups; 2) the Neandertals sampled are not more closely related to Europeans than they are to other contemporary amHs groups; and, 3) Neandertals and amHs diverged some 465,000 years ago and have been evolving separately for a substantial length of time (Krings et al., 2000; Krings et al., 1999; Krings et al., 1997).

Thus, the genetic evidence is consistent with the results obtained from postcanine dental morphological analysis, which suggest that 1) Neandertals are much more divergent from amHs than are the most divergent amHs from each other; 2) Neandertals are not more closely related to contemporary (and Upper Paleolithic) Europeans than they are to other amHs groups; and 3) Neandertals and archaic *Homo sapiens* are part of a single lineage that can be traced back to perhaps 500,000 years ago (based on dating of the Mauer mandible). The phenetic cohesiveness and low degree of variation within the Neandertal postcanine dental sample is also in agreement with the close similarity of the three Neandertal mtDNA samples that have been sequenced so far (Krings et al., 2000). These samples were obtained from individuals separated by thousands of miles and thousands of years and yet, like the Neandertals used in the dental analysis, they form a distinct cluster to the exclusion of all contemporary amHs.

In sum, the results of the phenetic and cladistic analyses of Neandertal relationships based on postcanine dental morphology are consistent with each other and are in line with those of other studies using different data sets and/or different methodology. While recognizing that sequencing and comparing mtDNA from early and Upper Paleolithic amHs is necessary for a more complete understanding of the relationships between amHs and Neandertals, the evidence collected thus far provide strong support for Neandertal distinctiveness.

SUMMARY AND CONCLUSIONS

Summary

In the past, research on the dentitions of Middle-Late Pleistocene hominids has focused on metrical comparisons or on comparisons of a few dental traits that seem to distinguish Neandertals from amHs (e.g., distinctive incisor morphology and taurodontism). In general, Neandertal postcanine teeth have been assumed to be much like our own.

This dissertation had two main goals. The first goal was to carry out a descriptive and comparative study of Neandertal postcanine dental morphology. The second goal was to use this information to determine the nature of the relationships among Middle-Late Pleistocene hominids and contemporary humans. To achieve these goals, data were first collected using the well-standardized and systematic methodology of the ASUDAS, to which additional dental traits identified in fossil hominids were added by the author. This was followed by a comparative and statistical analysis intended to determine in which ways Neandertal dental morphology is similar to, and in which ways it is distinct from, that of fossil and recent humans. Finally, quantified assessments of cladistic and phenetic relationships were made.

The purpose of the systematic and comparative study of Neandertal postcanine dental morphology was 1) to determine how Neandertal trait frequencies fit into the range of variation observed in other fossil and recent humans; and 2) to determine whether or not Neandertals exhibited dental traits that were unique to them. This study revealed that most of the dental traits observed in Neandertals and contemporary amHs are shared with

other fossil hominids. Where Neandertals differ from contemporary human groups is primarily in trait frequency rather than trait presence or absence. Many Neandertal dental trait frequencies fell outside the range observed in modern humans and some fell outside the range observed in other fossil hominids as well. A diagnostic Neandertal dental pattern emerged from this analysis. It includes 15 postcanine traits, some of which have been identified in previous work (Bailey, 2001; Coppa et al., 2001) and others that are newly identified here. Significantly, the Neandertal dental pattern (found in both early and late samples) does not conform to any pattern observed in contemporary or fossil amHs groups that were sampled.

The second objective of the comparative analysis was to test the hypothesis that Neandertals do not exhibit a significant number of dental autapomorphies, such that they could (or should) be excluded from the ancestry of anatomically modern humans (Hypothesis 1). The results suggest that a number of traits are either synapomorphic for Neandertals and archaic *Homo sapiens* or autapomorphic for Neandertals alone. The high frequencies of the transverse crest on P_4 and large anterior fovea on M_1 are most likely Neandertal/archaic *Homo sapiens* synapomorphies, rather than characters that are uniquely derived in Neandertals. However, the high frequencies of the lower molar mid-trigonid crest (especially its occurrence on M_2 and M_3) and asymmetry of P_4 are likely Neandertal autapomorphies. Other characters (the skewed upper molar shape with internally placed cusps) may be unique to Neandertals but this could not be statistically tested due to small sample sizes.

The second goal of this study was to use the information obtained from the comparative analysis to clarify the nature of the relationships among Middle-Late Pleistocene hominids and contemporary humans. In this context I tested two additional hypotheses generated from the Multiregional Evolution model (MRE) for modern human origins.

If, as suggested by MRE (Wolpoff et al., 1994), the differences between Neandertal and amHs dentitions simply reflect distinction along the lines of geographic races, then in a cladistic analysis Neandertals should be expected to emerge as a sister group to amHs, supporting their close phylogenetic relationship and recent common ancestor (Hypothesis 2). Previous cladistic analyses using non-dental data have reached ambiguous conclusions. For example, Pearson (1993) found support for the hypothesis that Neandertals and amHs represent separate taxa, but Stringer's (1987) cladistic analysis failed to resolve the phylogenetic relationship between Neandertals and amHs. Previous dental studies have noted substantial differences in the trait frequencies of Neandertals and contemporary amHs (Bailey, 2000a; Bailey and Turner, 1999; Irish, 1998). However, which group represents the more derived pattern was not determined.

The results of the cladistic analysis do not support an especially close phylogenetic relationship between Neandertals and amHs. Instead, a distinct Neandertal/archaic *Homo sapiens* clade is preserved in all 26 of the most parsimonious trees. In not one of these trees do Neandertals emerge as the sister group of amHs. The fact that the archaic *Homo sapiens* and Neandertal samples emerge as sister groups is

consistent with the hypothesis that they share a more recent common ancestor with each other than either does with amHs (see below for further discussion).

Another postulate of MRE is that Neandertals made a considerable contribution to the evolution and genetic makeup of amHs. Specifically, this hypothesis predicts that Neandertals will be more similar in their dental morphology to recent Europeans and Upper Paleolithic Europeans than they are to other recent geographic populations (Hypothesis 3). This prediction was not supported by an analysis of biological distance based on the Mean Measure of Divergence (MMD) statistic. MMD values between Neandertal samples and both Upper Paleolithic and recent European samples were very high and significant. Pair-wise comparisons show that rather than being *more* similar, the recent European sample was among those *least* similar to the Neandertal samples. This is not surprising given that the Neandertal dental pattern is characterized by traits that contribute to tooth crown complexity (see section on Postcanine Morphology and Morphometrics), while contemporary Europeans are characterized by a dental pattern that emphasizes structural simplicity rather than complexity (Mayhall et al., 1982). As regards the Neandertal-Upper Paleolithic European relationship, MMD values do not suggest a close biological relationship. In fact, the Neandertal samples are more similar to *Homo erectus* and early amHs samples than they are to the Upper Paleolithic sample.

Analysis of temporal change did suggest that late Neandertals are more like Upper Paleolithic amHs than are early Neandertals. However, this is not particularly strong evidence in support of MRE, as late Neandertals are also more like *Homo erectus* than are early Neandertals. Previous results suggest that late Neandertals are slightly less

dentally specialized than early Neandertals (Bailey and Turner, 1999), but the phenetic analysis suggests that they were not changing specifically in the direction of Europeans (recent or Upper Paleolithic). The slight change in MMDs from earlier to late Neandertal samples is overshadowed by the fact that the phenetic distance between the late Neandertal sample and the Upper Paleolithic European sample is much greater than that of two contemporary human populations separated by large geographic distances. Moreover, the dental evidence suggesting morphological continuity between European archaic *Homo sapiens* and Neandertals, as well as gradual evolution toward the Neandertal pattern within Europe, attests to deep roots for the Neandertal lineage within Europe.

Archaic Homo sapiens and Neandertal relationship

The results supporting a strong phenetic and cladistic relationship between European archaic *Homo sapiens* and Neandertals is interesting in light of discussions regarding the role of archaic *Homo sapiens*/*Homo heidelbergensis* in the evolution of Neandertals and anatomically modern *Homo sapiens* (see Rightmire, 1998). Related to arguments over which fossils should be included in this group - both African and European, or only European – is the debate about whether archaic *Homo sapiens* represents a group close to the last common ancestor of Neandertals and amHs (Groves and Lahr, 1994; Rightmire, 1990; Stringer, 1985; Stringer, 1993a) or a more specialized group that has a specific affinity to Neandertals (Condemi, 1996; Hublin, 1996; Rosas and Bermúdez de Castro, 1998; Vandermeersch, 1985).

In this dissertation a multivariate analysis of dental morphology showed that the archaic *Homo sapiens* sample (represented here only by European specimens) is phenetically indistinguishable from the Neandertal samples. While the low MMDs between archaic *Homo sapiens* and *Homo erectus* samples indicate that the former are dentally intermediate between the latter and Neandertals, the cladistic analysis unambiguously links archaic *Homo sapiens* with both early and late Neandertal samples. Individually, the fossils that comprise this small sample present a mosaic pattern of dental morphology: some (Arago 28) exhibit Neandertal apomorphies while others (Arago 13, Mauer) seem to lack them. This kind of mosaic pattern is found in cranial features as well (Cook et al., 1982; Stringer, 1981; Trinkaus, 1982). The small size and inexact chronology (Cook et al., 1982) of the archaic *Homo sapiens* sample require that any evolutionary interpretation be made cautiously. However, the dental evidence available tentatively suggests that there is there is gradual evolution towards the Neandertal dental condition in Europe. It is also consistent with the hypothesis that European archaic *Homo sapiens* is more accurately interpreted as an early representative of the Neandertal lineage than as a common ancestor to Neandertals and amHs. The forthcoming results of the study of the Sima de los Huesos (*Homo heidelbergensis* from Atapuerca, Spain) teeth by Martinón-Torres should be most informative in this regard.

Although the species issue was not a primary focus of this dissertation, it is worth noting how these data fit into current hypotheses. The results of the cladistic and phenetic analyses are consistent with the hypothesis that archaic *Homo sapiens*/*Homo heidelbergensis* is best interpreted as an early representative of the Neandertal lineage. If

they are, in fact, a chronospecies (Rosas and Bermúdez de Castro, 1998) of Neandertals (they evolved into Neandertals through anagenic evolution), then it may be appropriate to refer to them as early Neandertals rather than as a distinct species (*Homo heidelbergensis*). Whether or not Neandertals should then be considered a species distinct from *Homo sapiens* is more a matter of interpretation than fact. The combined findings of a distinct Neandertal dental pattern and probable Neandertal dental autapomorphies are consistent with the hypothesis that Neandertals represent a species (*Homo neanderthalensis*) distinct from *Homo sapiens*, but none of the results presented here requires that it be true.

Implications for modern human origins

Multiregional Evolution

Dental evidence presented here provides no direct support for the hypothesis that MRE is responsible for the evolution of modern human dental morphology in Europe: there is no evidence of a close phenetic or cladistic relationship between Neandertals and amHs, nor is there evidence of gradual evolution toward the modern human dental condition. The late Neandertals like Amud, Kůlna and Vindija, all possess (in what is preserved) the Neandertal dental pattern elucidated in this dissertation. Moreover, Neandertal apomorphies are present in these specimens: the MTC in Amud and Vindija, the skewed M^1 in Kůlna and asymmetrical P_4 morphology in Amud.

An earlier study of temporal change in incisor morphology (Crummett, 1994; 1995) also showed no morphological trajectory from the Neandertal to the modern condition in Western Europe (with the caveat that data for Upper Paleolithic samples

were unavailable). According to Crummett (1995), a better case for gradual evolution could be made for Central Europe. She observed a trajectory of change (reduction) from the condition observed in Neandertals to that observed in Upper Paleolithic (Dolní Věstonice) and recent Central Europeans; however, this only holds true if *Homo erectus* (represented by Nariokotome) is not included in the analysis. If the incisor morphology observed in Nariokotome is considered to represent the primitive condition, the temporal pattern observed only exists if Neandertals are not included in the temporal sequence. As I have observed in this study, inclusion of the Neandertal sample produces a significant disruption in gradual evolution of the modern pattern.

While arguing that Neandertals made a significant genetic contribution to recent European populations, Wolpoff and colleagues have also pointed out that disproving continuity in one region (e.g., Europe) does not necessarily disprove MRE in its entirety (Caspari and Wolpoff, 1995; Wolpoff, 1995a; Wolpoff et al., 2000; Wolpoff et al., 1984). Multiregional evolution does not posit independent origins for geographic populations but rather envisions that the transition from archaic *Homo sapiens* to anatomically modern *Homo sapiens* happened in bits and pieces in different parts of the world and then mixed together though the process of gene flow. Certain geographic areas may have contributed more (e.g., Africa) or less (e.g., Europe) to this process.

Wolpoff (1995b) has further argued that any hypothesis involving hybridization or assimilation is a multiregional hypothesis. However, this lumping of hybridization and assimilation hypotheses with the MRE hypothesis is not the consensus view, and most researchers continue to distinguish between the extreme (RAO of Stringer et al. [1984]

and MRE of Wolpoff et al. [1984]) and more intermediate (Assimilation model of Smith et al. [(1989)] and Afro-European *sapiens* model of Bräuer [(1984)]) models (e.g., Relethford, 2001c; Stringer, 2001). Relethford distinguishes between replacement (RAO), regional coalescence (MRE) and Primary African origin hypotheses (Relethford, 2001c). The model he prefers (Primary African origin) is similar to Smith et al.'s (1989) and Bräuer's (1984) hypotheses, in that it views modern human anatomy as starting in Africa and then spreading out, mixing with (not replacing) archaics outside Africa. Therefore, much of the difference among these different hypotheses for modern human origins have to do with the degree of admixture/hybridization that occurred between archaic and amHs populations.

Admixture, hybridization and gene flow are difficult hypotheses to test in the fossil record, as the degree of admixture and expected results are not entirely clear. Studies of admixture among dentally distinct contemporary amHs populations may reveal how admixture between Neandertals and amHs may manifest itself in the dentition. Baume and Crawford (1978) have demonstrated that the degree of known European admixture (ranging from 16% to 40% European contribution) is reflected in dental trait frequencies in Mexican populations – those with higher degrees of European admixture show lower frequencies of dental traits that characterize unmixed Mexican populations (e.g., incisor shoveling). Similarly, a study of the deciduous dental morphology of Japanese-American "hybrids" demonstrates that the offspring of Japanese and American parents show morphology and trait frequencies that are intermediate between that of their parental populations (Hanihara, 1963). These studies demonstrate that 1) admixture

between dentally distinct groups is, in fact, evident from their dental morphology, and 2) this admixture shows up in intermediate trait frequencies and form. If the Neandertal contribution was of the same magnitude as in these examples it is not unreasonable to expect to see similar evidence of admixture in their dental morphology.

Unfortunately, data from some of the most important fossils with regard to the hybridization hypothesis (e.g., the latest Neandertals and earliest Upper Paleolithic amHs) were unavailable because either permission was not granted or the cheek teeth were not preserved well enough for study. Based on the specimens that were preserved and available, the results do not support that Upper Paleolithic amHs show morphological trait frequencies that are intermediate between Neandertals and recent Europeans. In addition, regional dental characters found in Neandertals do not appear to be present in Upper Paleolithic or recent European populations. While MRE may not require that recent populations share all their dental characters with their archaic predecessors we would expect them to share a few.

Recent African Origin

Overall, the results of this study conform to the expectations of the RAO model as it concerns Europe. One prediction of the RAO model is that early amHs will be more similar to other amHs than they are to Neandertals. This prediction is supported by the results of both the phenetic and cladistic analyses. In the phenetic analysis, the distances between the early amHs sample and all amHs (especially the Upper Paleolithic amHs) samples are smaller than they are between early amHs and Neandertal samples. Early amHs are, in fact, phenetically more similar to *Homo erectus* than they are to Neandertals

(to whom they are temporally closer). In the cladistic analysis a close phylogenetic relationship among all amHs was indicated by results showing that nine of the 11 most parsimonious trees (82%) grouped early amHs with other amHs rather than with the Neandertal/archaic *Homo sapiens* group.

Along the same lines, RAO predicts that contemporary populations will be more like early amHs from Africa/Near East than they are like archaic populations from their own geographic region. The dental data from Europe are consistent with this prediction – contemporary Europeans are phenetically more like early amHs from the Near East than they are like European Neandertals/archaic *Homo sapiens*.

Other possibilities

Although he does not dispute that the above evidence is consistent with a replacement model, Relethford contends that the same patterns of biological affinity described above may also be expected under some forms of multiregional evolution – specifically a "Primary African Origin" model (Relethford, 1999; 2001b). Relethford (and others) offer that because the long term population size was larger in Africa than elsewhere, Africa would have made the largest contribution to modern human morphology (Harpending et al., 1993; Relethford, 2001a; 2001b; Relethford and Jorde, 1999b). Assuming gene flow was primarily in one direction (out of Africa) Archaic humans would have been "genetically swamped" by emigrating early amHs. Subsequent to this "genetic swamping," geographically dispersed populations would accumulate morphological distinctiveness through genetic drift. In this way, contemporary amHs populations could have achieved their own morphological identity without losing all of

the ancient African morphology. Although Relethford concedes that the Neandertal contribution to modern Europeans may have been negligible (as little as one percent), he views his Primary African Origin model as being different from a speciation/replacement model (Relethford, personal communication, 2002).

Other researchers (e.g., Harpending et al., 1993; Lahr and Foley, 1994) have also been unsatisfied with the RAO model of Stringer and others (Cann et al., 1987; Stringer and Andrews, 1988). Specifically, they view it to be an insufficient explanation for human diversity. It is generally inferred from the RAO model of Stringer et al. (1984) that modern human diversification occurred after the dispersal of early amHs out of Africa. However, Lahr and Foley's (1994) "Multiple Dispersal Model" and Harpending et al.'s (1993) "Weak Garden of Eden" hypothesis propose that modern humans leaving Africa had already diversified. Lahr and Foley's (1994) "Multiple Dispersal Model" holds that modern humans dispersed from Africa via multiple routes at different times. They believe that these ancestral populations were already differentiated prior to dispersing and that they experienced further differentiation subsequent to population growth and expansion after leaving Africa. Early differentiation was later overlaid by variation from subsequent dispersals and expansions. Harpending et al's (1993) "Weak Garden of Eden Hypothesis" proposes that genetic differentiation occurred in Africa prior to expansion, but that modern humans subsequently underwent a bottleneck around 100,000 years ago. This bottleneck, they propose, was followed by population subdivision and relative isolation of separate modern groups. Like the Multiple

Dispersals Model, this model also proposes that multiple demographic geographical expansions occurred at different times.

The results presented here are compatible with all of these "revised" RAO models. In particular, the finding that the Australian and African dental samples are very similar (also noted by Stringer et al., [1997]) is consistent with Lahr and Foley's hypothesis that the colonization of Australia occurred early and represents an early dispersal out of Africa. Their hypothesis is also consistent with my finding that Upper Paleolithic amHs are dentally quite distinct from recent Europeans. That Upper Paleolithic amHs and recent Europeans are morphologically distinct is supported by non-dental evidence as well (van Vark, 1990; van Vark et al., 1992). It is likely that Upper Paleolithic amHs represent more recent African emigrants that had not begun to differentiate toward European condition morphologically. Subsequent population movements (and resulting gene flow) prior or subsequent to the Neolithic are likely superimposed on this earlier variation.

In conclusion, I consider the results of this dissertation to be inconsistent with strict predictions derived from the MRE hypothesis and broadly supportive of the RAO hypothesis. However, in recent times the distinction between MRE and RAO has become somewhat hazy, such that the primary difference between these two hypotheses (as they are applied to Europe) is not whether or not admixture between Neandertals and amHs occurred, but rather, how significant the admixture was. Supporters of MRE view the admixture as substantial, whereas supporters of RAO view it to be trivial. From the viewpoint of the postcanine dentition, the degree of admixture between Neandertals and

amHs was insignificant, being either absent or negligible, and essentially had no long-term effect on modern human dental morphology.

APPENDIX A

THE ARIZONA STATE UNIVERSITY DENTAL ANTHROPOLOGY SYSTEM

TRAITS USED IN THIS STUDY

HYPOCONE (HYP: M^1, M^2, M^3): The presence of the distolingual cusp (Cusp 4). Presence = Grades 2-5. [Reference Plaque.]

CUSP 5 (C5: M^1, M^2, M^3): The presence of a fifth cusp (metaconule) that occurs between the metacone (Cusp 3) and hypocone (Cusp 4). Presence = Grades 1-5. [Reference Plaque.]

CARABELLI'S CUSP (CARA: M^1, M^2, M^3): A cingulum derivative that occurs on the lingual surface of the protocone (Cusp 1). Expression ranges from a faint ridge/groove to a large cusp with a free apex. Presence = Grade 2 (Y-shaped depression) to Grade 7 (large, free cusp). [Reference Plaque.]

PARASTYLE (M^1, M^2, M^3): A cingulum derivative that occurs on the buccal surface of the paracone (Cusp 2) or (less frequently) on the buccal surface of the metacone (Cusp 3). Expression ranges from a pit to a large cusp with a free apex. Sometimes referred to as a paramolar tubercle. Presence = Grades 1-5. [Reference Plaque.]

LINGUAL CUSP NUMBER (PLC: P_3, P_4): Number and relative size of the lingual cusps. Presence = Grades 2-9. [Reference Plaques.]

GROOVE PATTERN (YPAT: M_1, M_2, M_3): A "Y" pattern occurs when Cusps 2 and 3 are in contact, a "+" pattern when Cusps 1 through 4 are in contact, and an "X" pattern when Cusps 1 and 4 are in contact. [No Reference Plaque.]

ANTERIOR FOVEA (AFOV: M_1, M_2, M_3): Presence of a triangular depression distal to the mesial marginal ridge. The mesial accessory ridges of the protoconid and metaconid form the distal boundary of the depression. Presence = Grades 1-4.

CUSP NUMBER (4CSP: M_1, M_2, M_3): The number of cusps present. The tooth may have four cusps (protoconid, metaconid, hypoconid, entoconid), five cusps (hypoconulid also present), or six cusps (entoconulid also present). Cusp number does not include Cusp 7 (metaconulid). [No Reference Plaque.]

DEFLECTING WRINKLE (DW: M_1): The presence of a distally deflected (instead of straight) medial ridge on Cusp 2. Presence = Grades 1-3. [Reference Plaque.]

DISTAL TRIGONID CREST (DTC: M_1, M_2, M_3): A ridge or crest that connects the distal aspect of Cusps 1 and 2. Presence = Grade 1. [Reference Plaque.]

CUSP 5 (C5: M_1, M_2, M_3): The hypoconulid is the distalmost cusp situated between the entoconid and hypoconid. Presence = Grades 1-4. [Reference Plaque]

CUSP 6 (C6: M_1, M_2, M_3): The entoconulid or *tuberculum sextum* is a supernumerary cusp on the distal aspect of the tooth between the hypoconulid and entoconid. Presence = Grades 1-4. Size is scored relative to Cusp 5 (e.g., smaller, same size, larger). [Reference Plaque.]

CUSP 7 (C7: M_1, M_2, M_3): The *tuberculum intermedium* or metaconulid occurs on the lingual aspect of the tooth between the metaconid (Cusp 2) and entoconid (Cusp 4). Presence = Grades 1-4. [Reference Plaque.]

APPENDIX B

SCORE SHEET FOR THE ARIZONA STATE UNIVERSITY DENTAL ANTHRPOLOGY SYSTEM

APPENDIX C

SUPPLEMENTAL TRAITS USED IN THIS STUDY

PREMOLAR ACCESSORY RIDGES (Scott and Turner, 1997) or MaxPAR (Burnett, 1998) (P^3, P^4): The presence of accessory ridges on the buccal and lingual cusps of upper premolars. Degree of expression and location (buccal/lingual and mesial/distal) is scored. Expression ranges from absence (Grade 0) to marked (Grade 3). Presence = Grades 1-3. [Reference Plaque]

BUCCAL ESSENTIAL CREST PRESENCE AND FORM (P^3, P^4): Presence of the essential crest on the buccal cusp. Expression ranges from absence (Grade 0) to marked (Grade 3). Form may be a single ridge (Grade 1) or a bifurcated ridge (Grade 2). [No Reference Plaque.]

LINGUAL ESSENTIAL CREST PRESENCE AND FORM (P^3, P^4): Presence of the essential crest on the lingual cusp. Expression ranges from absence (Grade 0) to marked (Grade 3). Form may be a single ridge (Grade 1) or a bifurcated ridge (Grade 2). [No Reference Plaque.]

ACCESSORY MARGINAL TUBERCLES (P^3, P^4): The presence of a mesial or distal accessory marginal tubercle in which the sagittal sulcus is strongly bifurcated at the mesial and/or distal marginal ridge resulting in a bulge or free-standing accessory tubercle on the marginal ridge. Presence = any expression of an accessory marginal tubercle. Position – mesial or distal – is noted. [No Reference Plaque.]

MESIAL ACCESSORY RIDGE (P_3, P_4): Presence of an accessory ridge on the mesiolingual border of the tooth. Presence = Grades 1-3. [Reference Plaque.]

DISTAL ACCESSORY RIDGE (P_3 , P_4): Presence of an accessory ridge on the distolingual border of the tooth. Presence = Grades 1-3. [Reference Plaque.]

TRANSVERSE CREST (P^3, P^4, P_3 , P_4): Presence of a crest or ridge connecting the buccal and lingual cusps. Also called the central occlusal ridge. Presence = Grades 1-3. [Reference Plaque.]

TRANSVERSE CREST FORM (P_3 , P_4): The transverse crest may be straight and uninterrupted or bifurcated with another ridge (distinct from the distal or mesial accessory ridges). Scored as single (Grade 1) or bifurcated (Grade 2). [No Reference Plaque.]

MESIAL LINGUAL GROOVE (P_3, P_4): Degree of expression of a groove on the mesial lingual aspect of the tooth. It occurs much more frequently on P_3 than on P_4. Presence = Grades 1-3. [No Reference Plaque.]

METACONID PLACEMENT (P_3, P_4): Position of the metaconid relative to mesial and distal crests of protoconid and position of protoconid apex. The metaconid may be mesial, medial or distal. The most frequency condition is a mesially placed metaconid. [No Reference Plaque.]

CROWN ASYMMETRY (P_3, P_4): Shape of the lower premolars. In occlusal view the tooth crown outline is scored as asymmetrical (trait presence) or symmetrical (trait absence). An asymmetrical tooth has a lingual cusp that appears mesially truncated. [Reference Plaque.]

MESIAL MARGINAL ACCESSORY TUBERCLES (M^1, M^2, M^3): Presence of a accessory tubercles of the mesial marginal ridge complex. (Scott and Turner, 1997). Expression ranges from absence (Grade 0) to marked (Grade 3). Presence = Grades 1-3. [No Reference Plaque.]

MID-TRIGONID CREST (M_1, M_2, M_3): The presence of a low enamel ridge that connects the mesial portions of the protoconid (Cusp 1) and metaconid (Cusp 2). This trait was added to the ASUDAS in 1993 (Wu and Turner, 1993), however the scoring system used here is different than the one used there. Here a MTC is present if it forms a continuous bridge between cusps 1 and 2. If it is intersected by the sagittal sulcus it is scored as a Grade 1 but is not counted as present. This is an important distinction as the continuous crest is exceedingly rare in modern humans. [Reference Plaque.]

APPENDIX D

SCORE SHEET FOR SUPPLEMENTAL DENTAL TRAITS USED IN THIS STUDY

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BIOGRAPHICAL SKETCH

Shara Elaine Bailey was born in Lansdale, Pennsylvania in 1966. She received her elementary education at West Point Elementary and her secondary education at Pennbrook and Penndale Jr. High Schools and North Penn High School. In high school in addition to regular studies, she also received training in commercial art. After completing high school in 1984 she first pursued a degree in art and later a degree in Psychology. In January 1990, after a four-year hiatus, she returned to Temple University and completed a dual degree in Psychology and Anthropology, graduating Summa Cum Laude in 1992. Her interest in dental anthropology led her to Arizona State University for graduate study in August 1992. She completed her Masters Thesis (Title: Population Distribution of the Tuberculum Dentale Complex and Anomalies of th Anterior maxillary Teeth) and received her Masters of Arts degree in May 1995. That same year, she entered into Arizona State University's Ph. D. Program to acquire a doctorate in physical anthropology (December 2002). She has authored and co-authored several published and presented anthropological papers. In 1999 she won the Albert A. Dahlberg Award for best student paper in dental anthropology. Dissertation research has taken her to numerous museums and institutions in Europe and the Near East, as well as various American institutions. She has been awarded grants for data collection and travel (totaling more than $15,000) from Arizona State University Department of Anthropology, Sigma Xi Scientific Research Association, National Science Foundation and the LSB Leakey Foundation. From May 1993 to May 1997 she served as a graduate teaching associate in the Department of Anthropology, Arizona State University. From August 1997 to May 2000 she lived in Flagstaff, Arizona and served as an adjunct faculty member at Northern Arizona University and Coconino Community College. From August 2000 to July 2001 she taught part-time at Arizona State University and Mesa Community College. In July 2001 she was awarded a scholarship form the P.E.O. (Philanthropic Educational Organization) Sisterhood for dissertation writing. She was also awarded a one-year internship (James Arthur Internship in Biological Anthropology) to work with Ian Tattersall at the American Museum of Natural History, New York. In August 2002 she accepted a postdoctoral position, under the direction of Bernard Wood, at the George Washington University, Washington, DC. She is a member of the American Association of Physical Anthropologists, the Paleoanthropology Society, the Dental Anthropology Association, Sigma Xi Scientific Research Association and the Honor Society of Phi Kappa Phi. She currently resides in Alexandria, Virginia.

Shara's Dissertation Haiku

She runs stats all day
Measuring the bumps on teeth
Reading life's secrets

-- Nancy Mahoney, December 2001