The evolution of non-metric dental variation in Europe

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Abstract: *The potential for dental morphology to answer questions about human evolution in the Middle to Late Pleistocene has only recently begun to be appreciated. Non-metric dental traits provide useful information for taxonomic diagnosis as well as for assessing biological relationships among living and ancient populations. This study uses dental morphology to assess temporal change in Europe.* Homo erectus *serves as the presumptive primitive condition for later humans and change over time is assessed by calculating estimates of divergence between groups based on the mean measure of divergence multivariate statistic. The samples include* Homo erectus *(n = 12), early modern humans from Africa and West Asia (n = 12), early Neandertals (n = 16), late Neandertals (n = 20), Upper Paleolithic Europeans (n = 28) and contemporary Europeans (n = 47). The results show a marked disruption in continuity from early modern to later modern humans when Neandertals are incorporated into the temporal sequence. If Neandertals are left out of the sequence the change in divergence values conforms to expectations for gradual evolution toward the modern human condition (e.g., distance values get progressively smaller through time). At minimum this should set to rest any idea that modern Europeans evolved directly from Neandertal ancestors. Late Neandertals are somewhat less 'specialized' than early Neandertals; the implications of this finding are discussed.*
Keywords: *Neandertals, Dental morphology, Teeth, Modern humans, Middle Paleolithic, Upper Paleolithic, Modern human origins.*

Die Entwicklung nicht-metrischer Zahnvariation in Europa
Zusammenfassung: Während die Zahnmorphologie schon seit längerer Zeit herangezogen wird, um Aussagen über die Evolution früher Menschenformen zu gewinnen, wird ihr Aussagepotential bei Fragen nach der Evolution der Menschen vom Mittelpleistozän bis in das Jungpleistozän, d.h. von *Homo erectus* bis zum frühen *Homo sapiens*, sowie bei Fragen nach ihren Beziehungen zueinander erst seit Kurzem ansatzweise gewürdigt. Besonders Untersuchungen an Neandertalern beschränkten sich in der Vergangenheit im Wesentlichen auf die Merkmale am Schädel und am postkranialen Skelett. Wurden Neandertalerzähne mit einbezogen, lag das Schwergewicht meist auf metrischen Merkmalen. Inzwischen wird deutlich, dass uns auch nicht-metrische Zahnmerkmale nützliche Informationen sowohl für taxonomische Analysen als auch zur Feststellung biologischer Beziehungen zwischen lebenden und früheren Populationen liefern.
Der vorliegende Beitrag verwendet die Zahnmorphologie, um Veränderungen im Laufe der Zeiten in Europa festzustellen. Es wird gezeigt, dass man mittels nicht-metrischer zahnmorphologischer Merkmale in der Lage ist, im Allgemeinen verschiedene Taxa voneinander zu unterscheiden, oder, im Speziellen, Neandertalerzähne von Zähnen moderner Menschen (und denen anderer Menschen). Von besonderer Bedeutung ist diese Frage gerade deshalb, weil Zähne oft die einzigen erhaltenen Menschenreste sind und somit die einzigen Anhaltspunkte für die Zuweisung einer Fundstelle zu einer bestimmten Menschenform bieten. Einige der Merkmale, die in der Untersuchung eine besondere Rolle spielen, sind die Zahl, Anordnung und Ausprägung der Zahnhöcker der Backenzähne und Vorbackenzähne, die Ausprägung der Backenzahnfurchen sowie die schaufelförmige Ausprägung der oberen Schneidezähne. Die Verhältnisse bei *Homo erectus* dienen bei der Untersuchung als mutmaßliche Ausgangsverhältnisse für die Entwicklungen bei späteren Menschen, und Veränderungen durch die Zeit werden durch Errechnen von Schätzwerten für die Verschiedenheit zwischen Gruppen mittels komplexer statistischer Methoden ermittelt. Die untersuchte Stichprobe umfasst *Homo erectus* (12 Individuen), frühe moderne Menschen aus Afrika und Westasien (12 Individuen), frühe Neandertaler (16 Individuen), späte Neandertaler (20 Individuen), jungpaläolithische Europäer (28 Individuen) und zeitgenössische Europäer (47 Individuen).

Geht man von der Stichprobe der zeitgenössischen Europäer aus, so zeigt sich die größte Übereinstimmung mit den jungpaläolithischen Europäern, die zweitgrößte mit den frühen modernen Menschen, die drittgrößte mit *Homo erectus*. Die größten Unterschiede bestehen zu den frühen und späten Neandertalern. Ausgehend von den jungpaläolithischen Europäern sind ebenfalls die Übereinstimmungen mit den zeitgnössischen Europäern sowie mit *Homo erectus* und den frühen modernen Menschen relativ groß, während sich gegenüber den frühen und späten Neandertalern erneut große Unterschiede zeigen. Die frühen modernen Menschen sind in Bezug auf die Zahnmorphologie *Homo erectus* am ähnlichsten, gefolgt von den Jungpaläolithikern sowie, mit größerem Abstand, den zeitgenössischen Europäern und schließlich, mit noch größerem Abstand, den Neandertalern. *Homo erectus* ist den frühen modernen Menschen am ähnlichsten, gefolgt von den Jungpaläolithikern. Mit großem Abstand folgen die zeitgenössischen Europäer und die späten Neandertaler, während die größten Abweichungen zu den frühen Neandertalern bestehen. Sowohl die frühen als auch die späten Neandertaler sind am wenigsten verschieden von *Homo erectus*, gefolgt von den frühen modernen Menschen und den Jungpaläolithikern. Die größten Unterschiede bestehen zu den zeitgenössischen Europäern. In jedem Falle sind die Neandertaler, sowohl die frühen als auch die späten, stets die am weitesten von jeder der anderen Gruppen entfernte Gruppe. Die Unterschiede in der Zahnmorphologie zwischen Neandertalern und den anderen Gruppen nehmen im Laufe der Zeit zu, wobei die späten Neandertaler etwas weniger entfernt von den anderen Gruppen, d.h. etwas weniger ‚spezialisiert' sind als die frühen Neandertaler. Fasst man die Einzelergebnisse zusammen, so zeigt sich eine deutliche Unterbrechung in der Kontinuität von frühen zu späten modernen Menschen, wenn die Neandertaler in die zeitliche Abfolge integriert werden. Wenn man die Neandertaler nicht berücksichtigt, entspricht die Änderung im Maß der Verschiedenheit den Erwartungen an eine graduelle Evolution hin zu den Verhältnissen beim modernen Menschen. Dieses Ergebnis widerspricht dem Gedanken, dass die modernen Europäer direkt aus den Neandertalern hervorgegangen seien. Einiges spricht dafür, in den Neandertalern und den modernen Menschen unterschiedliche Arten zu sehen, doch bedarf es weiterer Untersuchungen an zusätzlichen Fossilien frühjungpaläolithischer moderner Menschen, um das Verhältnis zwischen Neandertalern und modernen Menschen besser verstehen zu können.
Schlagwörter: Neandertaler, Zahnmorphologie, Zähne, Moderne Menschen, Mittelpaläolithikum, Jungpaläolithikum, Ursprung moderner Menschen

Introduction

Teeth are durable structures that preserve very well in the archaeological and fossil record. Dental anthropologists have long appreciated teeth for what they can tell us about the lives of past peoples. Pathological conditions (e.g., periodontal disease, caries) can provide information on health, diet and even social status of individuals (Cucina and Tiesler 2003; Eshed et al. 2006; Hillson 1979). Dental eruption status can provide information on age of death of juveniles and macroscopic tooth wear can provide information on age of death of adults (e.g., Brothwell 1981; Smith 1991). Microscopic tooth wear provides information on what an individual was eating close to the time of its death (Teaford and Lytle 1996). Finally, forensic anthropologists have long used teeth to help identify individuals (Pretty and Sweet 2001).

Paleoanthropologists, too, have long appreciated teeth for the important information they can provide about human evolution. For the most part, efforts have concentrated on issues involving earlier hominins, such as the implications of canine size and dimorphism for behavior and social structure of early hominins (e.g., Plavcan and van Schaik 1997). Tooth wear, size and morphology also have provided important information on the diets of early hominins (e.g., Ungar and Grine 1991; Wood and Strait 2004); and tooth morphology has been even used to work out early hominin phylogeny (e.g., Grine 1985; Strait and Grine 2004).

Comparatively little research has made use of dental morphological variation to investigate questions about the evolution of, and relationships among, later humans (*Homo erectus* through early *Homo sapiens*). Studies of Neandertals, in particular, have focused primarily on cranial and post-cranial skeletal anatomy (Bookstein et al. 1999; Holliday 1997; Hublin 1978; Rosenberg 1988; Smith 1984; Trinkaus 1981). Until recently, those Neandertal studies that have utilized the dentition have focused mainly on tooth size and the trend for dental reduction during the Later Pleistocene (e.g., Brace et al. 1987).

There are a number of ways in which dental morphology can be used to answer important questions about the later stages of human evolution (i.e., during the Middle and Late Pleistocene). To begin, one must answer a very basic question: In the absence of other material, can teeth, alone, be used to identify taxa? Or more specifically: Can we distinguish Neandertal teeth from those of modern humans (and other hominins)? Once this has been established, changes in dental morphology across space and time can be used to answer microevolutionary questions, specifically: Do we observe evolution towards the modern human condition in particular areas of the world? and/or: Do we see evidence of admixture (gene flow) between archaic and modern humans? Finally, dental morphology may also be used to address the taxonomic status of a hominin. With regard to Neandertals the question is: Were Neandertals a species distinct from *Homo sapiens*?

Not surprisingly, these last two questions are linked. If Neandertals were simply a geographic variant of *Homo sapiens* that contributed extensively to the modern human gene pool we would expect to see either (a) gradual evolution from archaic (e.g., Neandertal) to the modern human condition in Europe or (b) evidence of admixture between Neandertals and the earliest modern Europeans (e.g., Upper Paleolithic). If, on the other hand, Neandertals were a species distinct from *Homo sapiens* then we would expect to see different evolutionary trajectories in the *Homo sapiens* and *Homo neanderthalensis* lineages. Moreover, if Neandertals were a species distinct from *Homo sapiens* interbreeding the two would have been trivial, at best, and most likely limited to sterile hybrids. As a result, we should see no particularly close relationship between Neandertals and Upper Paleolithic Europeans.

In this paper I will first review the potential of using teeth as a resource for identifying fragmentary human remains. From this foundation, I will then address the second and third questions regarding the microevolution in the later Pleistocene of Europe and what this means for the specific status of Neandertals.

Using teeth to identify Neandertals

One of the first steps in any analysis of fossil hominins must be correctly identifying the taxonomic group to which a fossil belongs. Based on dates for the early Aurignacian (presumably made by anatomically modern humans: Bailey and Hublin 2005), and dates for some of the last Neandertals (Higham et al. 2006; Hublin et al. 1995), there was a period of some 3,000 to 5,000 years in which Neandertals and modern humans overlapped in Europe after 35,000 BP. It is likely that the two groups were also coeval in the Levant some kyr ago (McDermott et al. 1993). Therefore, human fossils found dating to these periods of overlap could potentially belong to more than one hominin taxonomic group. While it would be convenient if paleoanthropologists always had complete skeletons, skulls or even complete dentitions with which to work, this is rarely the case. More often than not, what are uncorered in archaeological excavations are isolated teeth or perhaps a few teeth still preserved in a jaw. For this reason, one of the most useful applications of dental morphology to human evolutionary study is being able to identify taxa from fragmentary remains.

My research has focused on dental morphological variation in Neandertals and modern humans. It began with a basic question: Are Neandertal teeth qualitatively and quantitatively different from those of modern humans? In the first couple of decades following Darwin's publication of the *Origin of Species* (Darwin 1859) paleoanthropologists were mainly concerned with establishing a link between fossil hominins and humans. The primary goal of many of these studies was to determine whether a fossil was human-like or ape-like (see, for example, Weidenreich 1937; in this publication on the fossils from Zhoukoudian, comparisons were made with humans and apes). Although researchers recognized that Neandertal teeth were clearly different in some respects from those of modern humans (Gorjanović-Kramberger 1906), under this paradigm (i.e., Is it ape-like or is it human-like?) Neandertals were interpreted as having human-like teeth, thus establishing a closer affinity to humans rather than apes (Boule and Vallois 1957). There were those who felt that the morphological eccentricities of Neandertal teeth (e.g., taurodont molars with prismatic roots; see Figure 1) and skull suggested that they were, in fact, different species (e.g., Keith 1913). Nonetheless, until recently it is the first interpretation of Neandertal teeth (that there are no diagnostic differences) that has been more widely accepted (Henry-Gambier et al. 2004; Smith 1976).

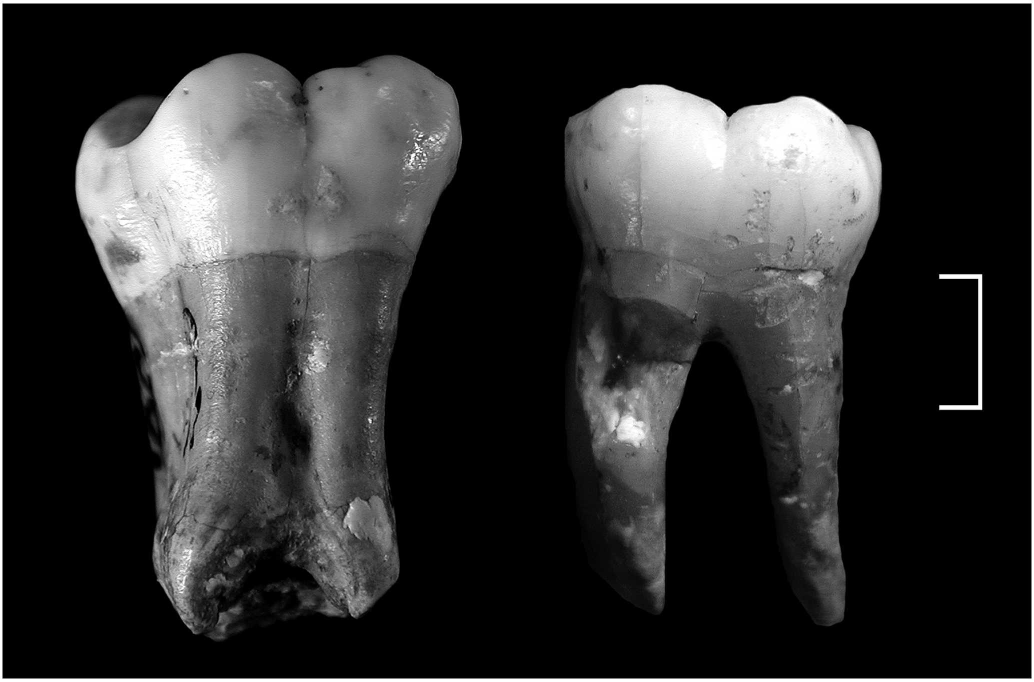

Fig. 1: *An example of a taurodont Neandertal molar from Krapina, Croatia (left) and a non-taurodont modern human molar from Les Rois, France (right). Taurodont refers to the enlarged pulp chamber housed by the roots that are joined near their apicies. Scale is 5mm.*

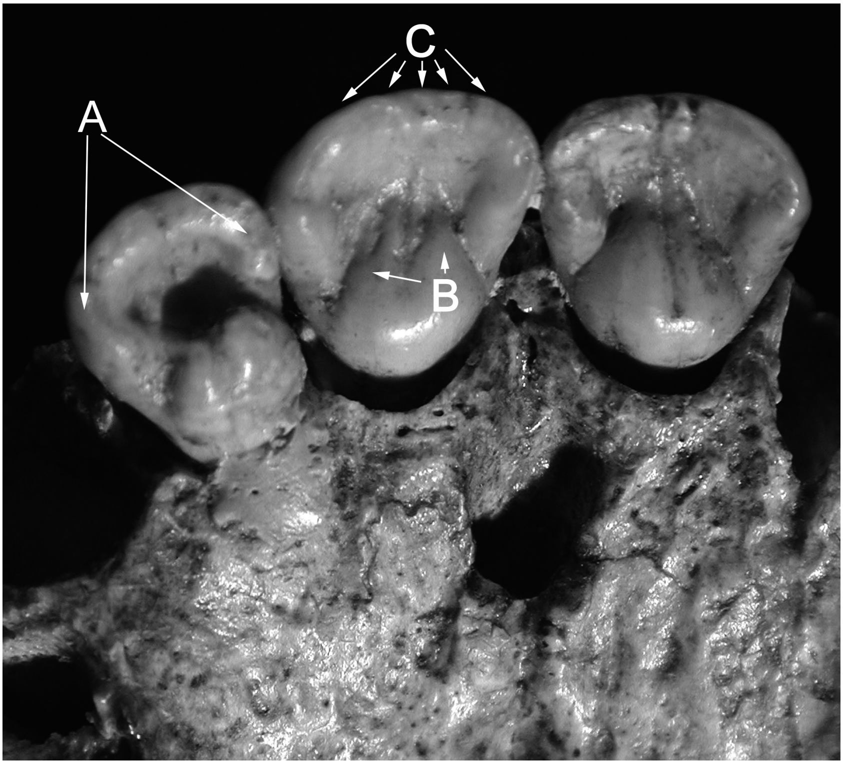

Fig. 2: *Unusual Neandertal incisor morphology from the Krapina site. The combination of marked shoveling (A), lingual tubercles (B) and labial convexity (C) is distinctive in Neandertals.*

Unusual incisor morphology (Figure 2) was one of the things that most impressed Gorjanović-Kramberger (1906) about the Krapina Neandertal teeth. This combination of marked lingual tubercle and marginal ridge development was determined by Mizoguchi (1985) to be uniquely ”Neandertal”. Crummett (1994) added marked incisor convexity to this complex, although she was less inclined to see their distinctiveness as taxonomically sinificant.

The distinctiveness of Neandertal dental morphology goes beyond their shovel shaped incisors and taurodont roots (Bailey 2006a). In the past decade, the publication and dissemination of morphological standards for assessing crown and root morphology (e.g., Arizona State University Dental Anthropology System or ASUDAS: Turner et al. 1991), has led to comparative studies of dental trait frequency patterns of Neandertals and modern humans. Using these standards, Irish (1998) and Stringer et al. (1997) found high divergence values between Krapina Neandertals and contemporary humans. Using an expanded non-metric trait list, a larger Neandertal dataset and adding fossil modern humans to the analysis Bailey found even more striking differences between the two groups (Bailey 2002b, 2006a). Bailey also noted unique characters and combinations of characters that distinguish Neandertals from both fossil and contemporary modern humans, and which may be derived for the Neandertal lineage (Bailey 2002a, 2004b).

In sum, while the teeth of Neandertals and modern humans are similar, having been derived from a fairly recent common ancestor, they differ in three primary ways. The primary differences are in (a) the exceptionally high or exceptionally low frequencies of certain traits, (b) the marked expression of these and other traits and (c) the combination of certain traits in individual teeth (Bailey 2006a). The following is a summary of these characters.

Neandertal trait frequencies

Several contemporary human groups (and subsets thereof) show patterns of high and low frequency dental traits that distinguish them from other contemporary groups, e.g., Asians (Hanihara 1969), and subsets thereof (Hawkey 1998; Turner 1990); Europeans (Mayhall et al. 1982) and Sub-Saharan Africans (Irish 1993). Neandertals also possess a unique pattern of high and low frequency traits. They are notable not only because their pattern is unlike that of any contemporary modern human population but also because they are distinctive relative to other fossil human groups (Bailey 2002b; Coppa et al. 2001). Table 1 presents the Neandertal dental pattern in terms of these high- and low-frequency traits. It should be remembered that 'high' and 'low' are relative terms and what is a 'high' frequency for one trait may be considered 'moderate' or 'low' for another. For example, the highest frequency for the supernumerary distal cusp on the M^1 (Cusp 5) may be 50% in contemporary humans. Therefore, frequencies of 40% or above would be considered 'high'. If most contemporary humans, on the other hand, possessed this trait in 80-90% of the individuals, a trait frequency of 40% would be considered low.

High frequency traits	**Low frequency traits**
Incisor Shoveling – I^1, I^2	Double Shoveling I^1
Labial convexity – I^1, I^2,	Four cusped M_2
Tuberculum dentale – I^1, I^2	Three cusped M^2
Canine mesial ridge $\underline{C}$	Enamel extension M^1
Cusp 5 – M^1, M^2	Deflecting wrinkle – M_2
Carabelli's cusp - M^1, M^2	Distal trigonid crest – M_2
Mesial lingual groove – P3	Mesial lingual groove – P_4
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	

Table 1: *Low and high frequency traits in Neandertals. I = incisor, C = canine, P = premolar, M = molar. Number indicates witch tooth (first, second, etc.) and wich jaw (superscript = upper, subscript = lower).*

For several of these traits the frequencies found in Neandertals fall within the range of contemporary modern humans: Shovel shaped incisors (high), M_1 Cusp 6 (high), M_1 Cusp 7 (high), P_4 multiple lingual cusps (high), and I^1 double shoveling (low). For other traits Neandertals present frequencies that are either exceptionally high (Bushman's canine, M^1 Carabelli's cusp, M^1 Cusp 5, M_2 Y groove pattern, P_4 mesial metaconid, P_4 transverse crest, P_4 asymmetry, M_1 anterior fovea and M_1 mid-trigonid crest) or exceptionally low (M^2 hypocone absence and four-cusped M_2) relative to contemporary modern humans. When this unique trait pattern was compared to those of seven contemporary human groups using a multivariate statistic of biological distance (mean measure of divergence), Neandertals were significantly different from all contemporary human groups with no particular affinity to any (Bailey 2002b).

Neandertal trait expression

Beyond possessing a unique pattern of dental trait frequencies, Neandertals also show unusually marked expression of certain traits. For example, the starting point for studies of Neandertal dental morphology has typically been the ASUDAS (Bailey 2000; Coppa et al. 2001; Irish 1998). However, Crummett (1994:91) found it necessary to develop new scoring criteria for marginal ridge development (shoveling) and for lingual tubercle development (*tuberculum dentale*), partially in order to cover the range of variation observed in fossil hominins. In addition, I have noted that the labial curvature (or convexity) of incisors in Neandertals is often stronger than the highest grade on the ASUDAS reference plaques (Bailey 2000). Other teeth also show marked expression of certain traits in Neandertals. For example, asymmetry in the P_4 crown outline tends to be much stronger in Neandertals than it is in modern humans (Bailey and Lynch 2005). In addition, the mid-trigonid crest (a crest connecting the anterior cusps of lower molars) in Neandertals tends to be a thick, continuous crest, while in modern humans, when it is present, it is thin and/or is discontinuous, being separated by a sagittal fissure.

For the traits above, more often than not, there is a good deal of overlap between Neandertals and modern humans in the middle areas of trait expression. If we take as an example the occlusal asymmetry of the P_4 crown, one can find asymmetrical P_4s in modern humans and ovoid P_4s in Neandertals but when one examines the upper end of the range of expression, only Neandertals fall on one end of the extreme and only modern humans fall on the other (Figure 3). Similar results were recently obtained by Martinón-Torres et al. (2006) through a geometric morphometric study of the P_4.

Trait combinations

No doubt the most notable of differences between Neandertal and modern human dental morphology are the combinations of traits observed in certain teeth. The most diagnostic teeth are the upper incisors, upper first molar, lower fourth premolar, and lower molars (especially M_3).

In the previous section I noted that there are certain traits for which Neandertal trait frequencies fall within the range of those of modern humans. Lingual marginal ridge development (shoveling) is one of these. Like Neandertals, certain Asian-derived groups (including North East Asians and Native Americans) present high frequencies of well-

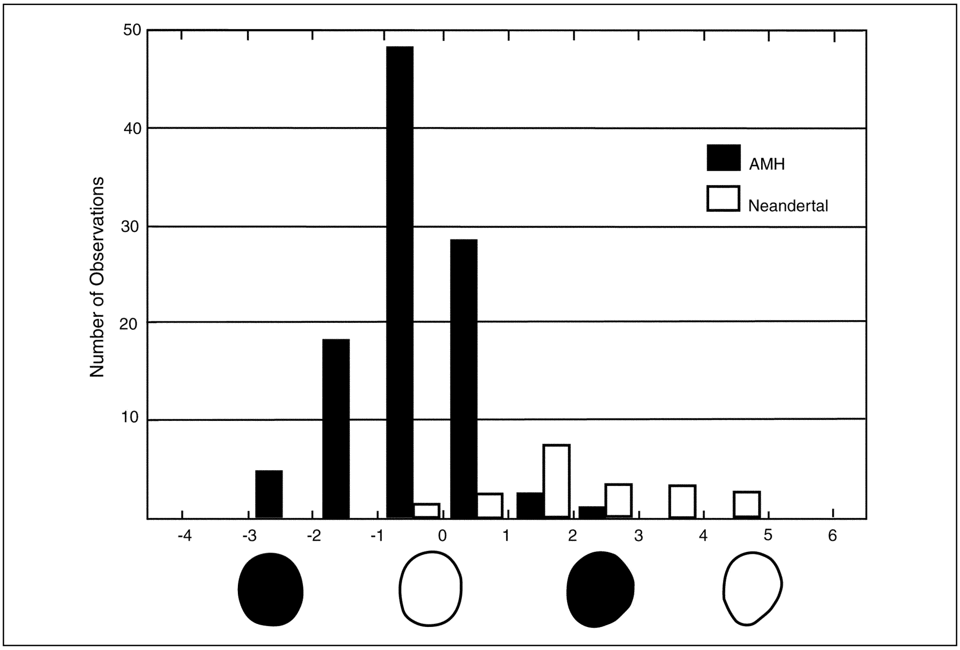

Fig. 3: *Range of variation in form of the lower fourth premolar (P_4). In modern humans (black) the crown tends to be round or ovoid. In Neandertals (white) the crown tends to be asymmetrical. While there is overlap in form, only Neandertals are on one end of the range of variation, and only modern humans are on the opposite end.*

developed shovel-shaped incisors (Hrdlička 1920; Scott and Turner 1997). However, in these groups the labial surface (towards the lips) is flat or slightly concave rather than convex, as observed in Neandertals (see Figure 4). The combination of strong shoveling, marked labial curvature and strong lingual tubercles is distinctive of Neandertals (Crummett 1994; Mizoguchi 1985).

Likewise, multiple lingual cusps are common on the lower fourth premolar of Neandertals. They are not uncommon in certain modern human groups (e.g., Australians); however, the combination of multiple lingual cusps, an asymmetrical crown and a transverse crest (connecting the buccal and lingual cusps) appears to be unique to Neandertals (Bailey 2002a). This tooth is so diagnostic, in fact, that one could potentially identify a Neandertal based on a single P_4.

The same concept applies to upper first molar crown shape as well. In particular, Neandertal upper first molars tend to present an exceptionally large hypocone (distolingual cusp). The size relationship between the two distal cusps – the hypocone, which is large, and the metacone, which is small – contribute to a skewed crown shape that is distinctive of Neandertals. Finally, the cusps of this tooth tend to be internally compressed, so that the occlusal basin is smaller than that of modern humans. This is so distinct that there is virtually no overlap between Neandertals and modern humans for this character (Figure 5). Thus far, the data indicate that the combination of these features is unique to Neandertals.

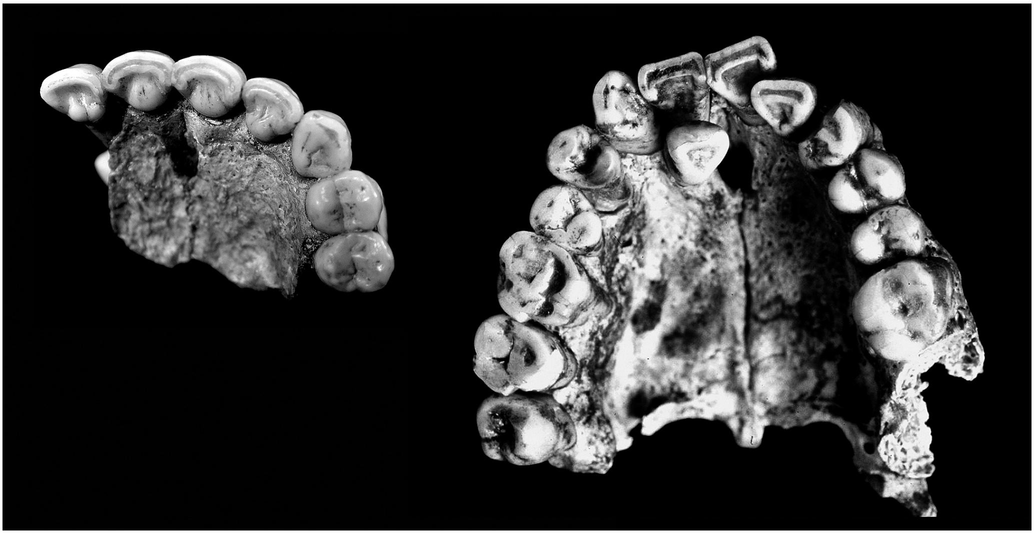

Fig. 4: *Two maxillae illustrating similar degrees of shoveling (lingual ridge development) but very different shapes in the incisors of a Neandertal (left) and an Asian-derived contemporary human (right). Note the markedly convex labial surface in the Neandertal.*

In sum, the recent work on Neandertal dental morphology has shown that

a) The Neandertal pattern of trait frequency is unlike that of any modern human group;

b) Neandertals are distinctive in their high frequencies and marked expression of certain dental crown traits, for which they fall outside the range observed in modern humans; and

c) Neandertals present, in high frequencies, certain trait combinations that are either absent or rare in modern humans.

While it would be ideal to have access to a complete dentition of unworn teeth when trying to identify human fossils, this is rarely the case. Luckily, certain isolated teeth can now be used to diagnose Neandertal vs. modern human with a high degree of accuracy (Bailey 2006b). Thus, contrary what some researchers claim (e.g., Henry-Gambier et al. 2004), teeth can provide important information for distinguishing among fossil hominids of the Middle – Late Pleistocene.

Temporal change in dental morphology

Once the taxonomic assignment of fossils of interest is secure, it is possible to examine dental morphological change over time. One way to ascertain temporal change is to examine the divergence in dental patterns in human groups representing different time periods, especially in the same geographic area. Studies like this have been undertaken in Africa (Irish 1993), India (Hawkey 1998) and parts of Asia (Turner 1992). Assessing morphological change in Europe, allows us to ascertain whether or not there is (a) gradual change in Europe from the archaic (e.g., Neandertal) to the modern human (e.g.,

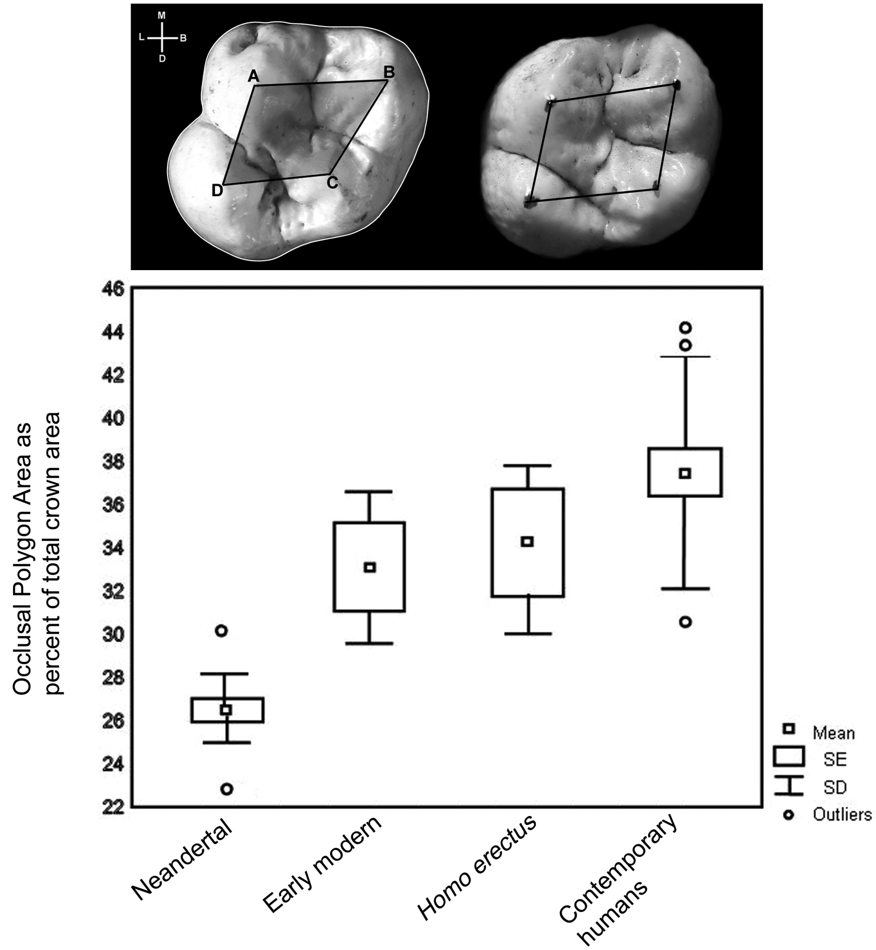

Fig. 5: *Illustration of the upper first molar in a Neandertal (left) and a modern human (right). The combination of unusual cusp proportions, skew of the tooth and the internal placement of the cusp tips are distinctive of Neandertals. The graph represents the size of the polygon circumscribed by the cusp tips relative to the crown base. It is very small in Neandertals and there is virtually no overlap between Neandertals and non-Neandertals.*

Upper Paleolithic and contemporary European) dental condition and/or (b) whether or not there is evidence of admixture between Neandertals and Upper Paleolithic Europeans. The answer to both of these questions has implications for the specific status of Neandertals.

If modern Europeans evolved through gradual evolution in Europe, one may expect divergence values to decrease between archaic (e.g., Neandertal) and modern (e.g., Upper Paleolithic and contemporary) European populations. In other words, populations should become more similar over time. Although there has not been an extensive amount of work done on 'hybridization' in human populations, some early studies indicate that when two dentally divergent populations mix, there is a convergence of dental morphological patterns (Baume and Crawford 1978; Hanihara 1963). Therefore, if there was significant gene flow between Neandertal and Upper Paleolithic European populations we may expect to see evidence of this in the dental morphology.

Crummett (1994) examined the first of these two hypotheses by investigating temporal change in incisor morphology. Her results found no morphological trajectory from the Neandertal to the modern condition in Western Europe (with the caveat that data for Upper Paleolithic samples were unavailable). However, she felt that a better case for gradual evolution could be made for Central Europe. This is because she observed a trajectory of change from the incisor form observed in Neandertals to that observed in Upper Paleolithic (Dolní Věstonice) and recent Central Europeans.

Crummett's study (1994) provides a basis for a more complete study including many more traits in the analysis, as well as larger samples of the earliest modern humans and *Homo erectus*. Either of these samples could represent the ancestral condition for later modern humans, and so provide a starting point for a study of change over time.

Methods

To estimate change over time I have examined divergence estimates, hypothesizing that if there was gradual evolution to the modern human condition, there should be a reduction of divergence values as groups converge temporally in Europe.

Analysis of divergence among groups requires a multivariate statistic. The Mean Measure of Divergence (MMD) statistic has been most commonly applied to questions of dental morphological affinity. The MMD utilizes multiple traits to provide a measure of dissimilarity among groups. Certain issues arise when using small sample sizes in MMD analysis (see Harris 2004 for a review). One of these is the risk of obtaining MMD values that are 0 or negative because the correction factor is larger than the MMD: the smaller the sample size the larger the correction factor. In order to control for this I have included only traits for which at least two groups differed by a minimum of 20%, and have used samples consisting of a minimum of three individuals. Certain traits, therefore, had to be eliminated from the analysis (e.g., Carabelli's cusp of the M^1). In addition, although the MMD program utilizes the Freeman and Tukey angular transformation to correct for small sample sizes (Berry and Berry 1967; Green and Suchey 1976; Sjøvold 1973), sample sizes of 3 to 7 individuals in some of the fossil groups are likely too small even for this correction. Therefore, it is important not to over-interpret the statistical significance of some of the MMD values.

This study utilizes 20 traits in the analysis (see Table 4). Those traits recommended by Turner et al. (1991) for population divergence analysis (traits 1-5, 7-9, 11, 14-19) are recommended because they are easy to score, can be scored even in worn teeth and because they vary among contemporary geographic populations. My research has shown that analyses of fossil humans based solely on these standards, which were developed for use on contemporary humans, leads to biased results, in which fossil groups appear more 'modern' because traits that are absent or invariable in contemporary human groups are not included in the analysis. Therefore, I have found it necessary to expand upon the ASUDAS and include traits that I have shown to be useful in distinguishing among fossil human groups (Bailey 2002b). In this study, these additional traits include P_3 mesial lingual groove, P_4 transverse crest, P_4 asymmetry and M_3 mid-trigonid crest. These traits are also easy to score, tend to be scorable even in moderately worn teeth, and their frequencies differ among fossil human groups, although they appear to be less variable in modern human populations.

Materials

This analysis includes samples of *Homo erectus*, modern humans and Neandertals (Table 2). The modern human and Neandertal samples were divided into temporal groups. The modern humans are represented by early modern humans from Africa and West Asia, Upper Paleolithic Europeans and contemporary Europeans. The early modern humans from Africa and West Asia sample, more or less, a similar time period as the early Neandertal group and potentially provide the alternative source for primitive traits observed in modern humans in Europe (and elsewhere). The Neandertals are represented by early (pre-70kyr) and late (post-70kyr) samples. *Homo erectus* is included to represent the probable primitive condition from which later human variation is derived.

The *Homo erectus* material consists of fossils from Java, Asia, North Africa and East Africa. With the exception of the North African fossils and those from Sangiran, all *Homo erectus* data were collected from high-resolution casts. All other observations (on Neandertals and modern humans) were made on original specimens.

Results

The MMD values for the pair-wise comparisons are presented in Table 3. All pair-wise comparisons between the contemporary European sample and fossil samples are significant, and four of the five MMD values are also quite high. The closest similarity to the contemporary European sample is with the Upper Paleolithic European sample (MMD = 0.169). The next closest affinity is with the early modern human sample (MMD = 0.406), followed by the *Homo erectus* sample (MMD = 0.684). The two Neandertal samples are the most dissimilar from the contemporary European sample. Although the later Neandertal sample is less dissimilar than the earlier Neandertal sample (MMD = 1.210 and 1.668 respectively), its distance is about twice as large as the distance between the *Homo erectus* sample and the contemporary European sample.

As regards the Upper Paleolithic sample, as above, all pair-wise comparisons are significant. The closest affinity is with the contemporary European sample (MMD = 0.169), and this is followed closely by the *Homo erectus* sample (MMD = 0.140). The early modern human sample is the next closest (MMD = 0.196). As was the case with the contemporary European sample, both early and late Neandertal samples are much more distant from the Upper Paleolithic sample (MMD = 1.218 and 0.810, respectively) than other fossil samples. In this case the Neandertal samples are four to six times more distant from the Upper Paleolithic sample than are all other samples.

The early modern human sample shows the closest affinity to the *Homo erectus* sample (MMD = 0.053, N.S.). All other MMD values are significant. The next closest affinity is with the Upper Paleolithic European sample (MMD = 0.196), followed much more distantly by the contemporary Europeans (MMD = 0.406), late and early Neandertals (MMD = 0.629 and 0.916, respectively).

Site	Max. No. Individuals	Site	Max. No. Individuals
Homo erectus			
Zhoukoudian	4	Rabat	1
Sangiran	6	West Turkana (KNM-WT)	1
Tighenif	2	East Rudolf (KNM-ER)	7
Thomas Quarries	1	Olduvai	2
Sidi Abderrahman	1	Dmanisi	1
Neandertals			
Early			
Ehringsdorf	5		
Krapina	38		
Malarnaud	1		
Pontnewydd	14		
Late			
Arcy-sur-Cure (Mousterian)	7	Monsempron	2
Chateauneuf 2	1	Montgaudier 5	1
Ciota Ciara (Monte Fenera)	2	Obi Rakhmat	1
Combe Grenal	1	Ochoz	1
Devil's Tower, Gibraltar	1	Petit-Puymoyen	7
Grotta Taddeo	4	Regourdou	1
Guattari 3	1	Roc de Marsal	1
Hortus	6	Saccopastore	2
Kůlna	1	Spy 1, 2	2
La Fate	4	Taubach	1
La Ferrassie	1	Vindija	7
La Quina	3		
Modern Humans			
Upper Paleolithic Europeans			
Abri Blanchard	1	La Madeleine	1
Abri Labatut	1	Laugerie Basse	1
Abri Pataud	1	Les Vachons	1
Dolní Věstonice	7	Miesslingtal	1
Farincourt	2	Mladeč	3
Fourneau du Diable	1	Oase	2
Grotte des Rois	26	Oberkassel	2
Grotte des Abeilles	3	Pavlov	3
Isturitz	5	Pech de la Boissière	2
La Chaud	4	Roc de Combe 4	1
La Ferrassie	1	St Germain la Rivière	22
La Gravette	1		
Early Afro-Asian Moderns			
Die Kelders	10	Sea Harvest	1
Equus Cave	12	Qafzeh	7
Klasies River Mouth	6	Skhůl	4
Hoedjies Punt	3		

Table 2: *List of fossil hominin samples and maximum number of individuals used in this study.*

The *Homo erectus* sample has its closest affinity to the early modern human sample (as above) followed by the Upper Paleolithic European sample (MMD = 0.140). It is much more distant, and nearly equally so, from contemporary Europeans and late Neandertals (MMD = 0.684 and 0.600, respectively), and it is the most distant from early Neandertals (MMD = 0.870).

All pair-wise comparisons between Neandertal samples and other samples are high and significant. However, the early and late Neandertal samples do not differ significantly from one another (MMD = -.007). Early and late Neandertals (respectively) are least different from *Homo erectus* (MMD = 0.870 and 0.600), followed by early modern humans (MMD = 0.916 and 0.629), Upper Paleolithic Europeans (MMD = 1.218 and 0.810) and are the most different from contemporary Europeans (MMD = 1.668 and 1.210). In all comparisons, the Neandertal samples stand out as being the most distant from any group – fossil or recent. Although the late Neandertal sample tends to be less distant from these groups than does the early Neandertal sample, it maintains its distinctiveness. Figure 6 illustrates that the dental morphological distances between the Neandertal samples and other samples increases over time, and also that the late Neandertal sample is less distant from all groups than is the early Neandertal sample.

	HE	**EAAM**	**ENEAN**	**LNEAN**	**UPEUR**	**EUROP**
HE	0.0	0.053	0.870*	0.600*	0.140*	0.684*
EAAM		0.0	0.916*	0.629*	0.196*	0.406*
ENEAN			0.0	-.007	1.218*	1.668*
LNEAN				0.0	0.810*	1.210*
UPEUR					0.0	0.169*
EUROP						0.0

Table 3: *Mean measure of divergence values for pair-wise comparisons using among samples based on 20 non-metric dental crown traits (see text). HE –* Homo erectus*, EAAM – Early African/Asian modern, ENEAN – Early Neandertal, LNEAN – Late Neandertals, UPEUR – Upper Paleolithic European, EUROP – Contemporary European. Significant MMD values (p<0.05) are indicated with an *. The negative value for the ENEAN resulted from the MMD being smaller than the correction factor. Thus, the difference between these two samples is very small.*

Discussion

The primary purpose of this analysis was to ascertain whether or not there was a gradual evolutionary change in dental morphological trait frequencies towards the modern human condition in Europe during the later Pleistocene. If Neandertals played a significant role in modern human evolution in Europe we would predict that pair-wise comparisons between progressively more contemporaneous groups would decrease over time. Two alternative scenarios are tested:

1. The scenario in which *Homo erectus* represents the primitive condition and there is gradual evolution toward the modern condition through early Europeans (Africa and West Asia), Upper Paleolithic modern humans in Europe to contemporary modern Euro-

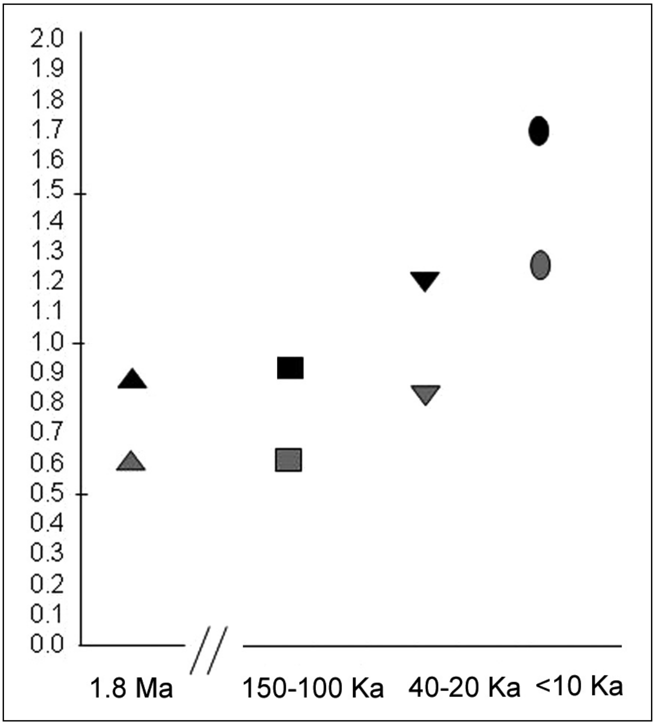

Fig. 6: *Early (grey) and late (black) Neandertal MMD pair-wise comparisons across time with:* Homo erectus *(triangles), early modern humans (squares), Upper Paleolithic Europeans (reversed triangles) and contemporary Europeans (ovals). The MMD values represent biological distances, which increase over time.*

peans. In this scenario, one can imagine Upper Paleolithic Europeans deriving from early African and/or West Asian modern humans and contemporary Europeans evolving from Upper Paleolithic Europeans (or some other closely related group) without significant influence from Neandertals.

2. The scenario in which *Homo erectus* represents the primitive condition and evolution toward the Upper Paleolithic (and later) modern European condition progressed either (a) though Neandertals directly or (b) with significant contribution from Neandertals.

Figure 7 illustrates the MMD values resulting from the dental comparison of fossil human groups to the contemporary European sample. This figure shows a gradual decrease in MMD values over time from *Homo erectus* to early modern humans to Upper Paleolithic Europeans, relative to contemporary Europeans. If we assume that the dental pattern of *Homo erectus* represents the primitive condition, then it seems much more parsimonious for the modern European pattern to have derived from *Homo erectus* through early moderns and Upper Paleolithic Europeans than through some incorporation of Neandertals in the scenario. Instead of being easily integrated into this scenario, when Neandertals are included there is an abrupt increase in the MMD values after *Homo erectus*.

The hypothesis of dental morphological continuity over time has been previously addressed, in part, by Crummett (1994) using incisor morphology. Crummett found a continuation of incisor morphologies from an early Neandertal shape through that displayed in Upper Paleolithic Europeans to the contemporary European form. However, this continuity required beginning from morphology unlike *Homo erectus* (Nariokotome in her study; Crummet 1994:192). In other words, it requires that *Homo erectus* not represent the primitive condition. The same could be said of the results from this analysis, which are based on many more dental traits. Starting with the early Neandertal sample there is a decrease in the distance between fossil and contemporary European samples, although it is far from gradual. The problem with interpreting this as evidence of regional continuity is that it requires that Neandertals rather than *Homo erectus* represent the primitive condition.

This analysis does not support this conclusion. If Neandertals possess a primitive dental pattern we would expect them to be more like *Homo erectus*, or early modern humans than they are. In fact, their dental pattern is among the least like *Homo erectus* and early modern humans. If Neandertals possess a primitive dental pattern we would not expect their dental pattern to be less like modern humans than is the *Homo erectus* dental pattern. Moreover, the fact that contemporary European and late Neandertal samples are nearly equidistant from *Homo erectus* but markedly different from each other, suggests that both patterns are derived relative to *Homo erectus*, which represents the primitive condition. It is clear from this that Neandertals do not make a good starting point for any study examining the evolution of modern human dental morphology; either *Homo erectus* or early anatomically modern humans, wich are much less derived from the primitive condition, make a better model.

Starting from either Homo erectus or early anatomically modern humans as the ancestral condition there is clear discontinuity in dental patterns from the earliest modern humans to later modern humans when Neandertals are part of the evolutionary sequence. While the later Neandertal sample's pair-wise comparisons with non-Neandertals are consistently lower than the earlier sample's comparisons (e.g., MMD values), both early and later Neandertal samples get increasingly more distant from modern humans over time (Figure 6). One can make a much stronger argument for continuous evolution from *Homo erectus* to modern Europeans, through early modern humans and Upper Paleolithic Europeans, as the relevant MMD values become consistently smaller over time.

Evolution from the Neandertal to the modern human pattern, therefore, is not supported with this data. However, few serious researchers subscribe to an 'evolution from Neandertals' scenario in Europe (but see Brace 1964). The archaeological and fossil evidence suggests that anatomically modern humans entered a European landscape occupied by Neandertals sometime after 50 kyr. In the past two decades the "Neandertal question" has shifted from being one of whether or not Neandertals evolved into modern humans to whether or not there was significant interbreeding between the two when they met (see papers in Conard 2006).

Admixture is a difficult hypothesis to test in the fossil record, as the expected results depend on the degree of genetic exchange and it is not entirely clear just what we should expect to find as evidence of this interbreeding. To this end, studies of admixture among

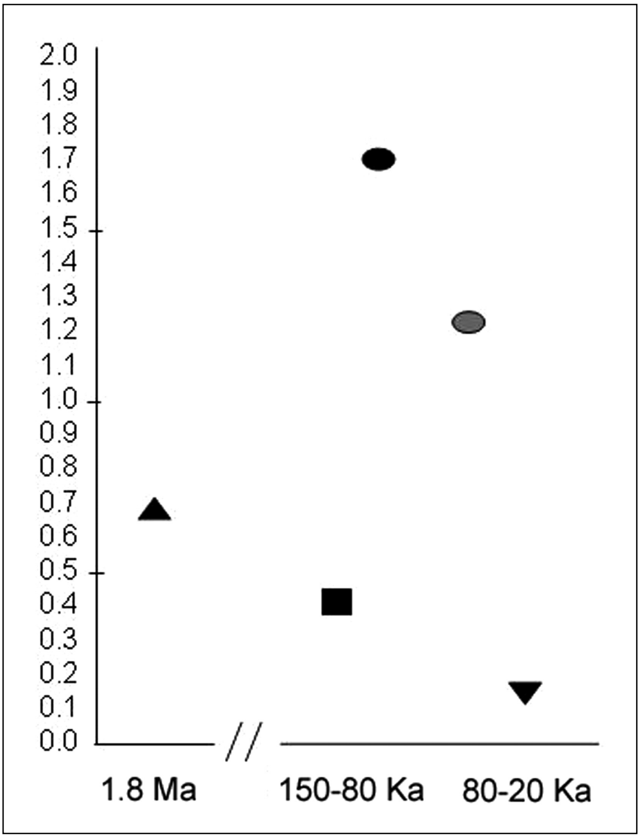

Fig. 7: *MMD values between fossil samples and the contemporary European sample. Biological distances gradually decrease over time from* Homo erectus *(triangle) to early modern humans (square) to Upper Paleolithic Europeans (reversed triangle). However, there is discontinuity in this pattern when early (black oval) and late (grey oval) Neandertals are incorporated into the temporal sequence.*

dentally distinct contemporary human populations may reveal how admixture between Neandertals and modern humans might be detected in the dentition. Baume and Crawford (1978) demonstrated that dental trait frequencies in Mexican populations reflect the degree of known European admixture (ranging from 16% to 40% European contribution) – those with higher degrees of European admixture show lower frequencies of dental traits that characterize unmixed Mexican populations (e.g., incisor shoveling). Similarly, Hanihara (1963) showed that the deciduous dental morphology of Japanese-American ”hybrids” show morphology and trait frequencies that are intermediate between that of their parental populations. These studies demonstrate that (1) admixture between dentally distinct groups can be detected in the dental morphology of their descendents/ offspring, and (2) this admixture manifests itself 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.

Trait	*Homo erectus*	Early African/ Asian modern	Early Neander-tals	Late Neander-tals	Upper Paleolithic Europeans	Contempo-rary Euro-peans
1) Labial convexity I^1 + = 2-4	60.0/5	50.0/8	100/14	85.7/7	20.0/15	11.8/17
2) Shoveling I^1 + = 2-6	100.0/5	33.3/6	100/14	100/7	45.5/11	37.5/16
3) Double shoveling I^1 + = 2-6	0.0/5	0.0/7	0.0/14	16.7/6	14.3/7	35.3/17
4) Tuberculum dentale I^2 + = 2-6	33.3/3	66.7/6	100/13	87.5/8	0.0/6	33.3/18
5) Bushman Canine $\underline{C}$ + = 1-3	20.0/5	0.0/5	33.3/12	57.1/7	16.7/6	0.0/16
6) Accessory cusp P^3 + = 1-2	25.0/4	42.9/7	60.0/10	60.0/10	40.0/5	36.6/41
7) Cusp 5 M^1 + = 1-5	33.3/3	40.0/5	63.6/11	77.8/9	53.3/15	30.5/36
8) Hypocone reduction M^2 + = 3-5	0.0/6	0.0/7	0.0/13	7.1/14	16.7/18	23.4/47
9) Lingual cusp number P_3 + = 2-9	0.0/7	16.7/6	7.7/13	29.4/17	0.0/12	40.0/35
10) Mesial lingual groove P_3 + = 1	58.3/12	25.0/4	77.8/9	50.0/12	41.7/12	42.9/35
11) Lingual cusp number P_4 + = 2-9	0.0/7	66.7/6	92.9/14	92.3/13	45.5/11	55.9/34
12) Transverse crest P_4 + = 1-2	35.7/14	16.7/6	100.0/13	85.7/14	25.0/12	17.6/34
13) Asymmetry P_4 + = 1-2	38.5/13	33.3/6	92.9/14	92.3/13	33.3/9	7.1/28
14) Deflecting wrinkle M_1 + = 2-3	66.7/6	75.0/4	0.0/11	6.7/15	17.6/17	8.3/12
15) Cusp 6 M_1 + = 1-4	28.6/7	0.0/7	25.0/8	46.2/13	21.1/19	8.3/24
16) Cusp 7 M_1 + = 2-4	41.7/12	41.7/12	26.7/15	10.0/20	3.7/27	3.3/30
17) Anterior Fovea M_1 + = 2-4	75.0/8	83.3/6	93.8/16	84.2/19	52.9/17	25.0/16
18) Y pattern M_2 + = Y	90.9/11	100/6	66.7/15	78.9/19	50.0/24	28.1/32
19) Four cusps M_2 + = 4	0.0/15	10.0/10	0.0/15	0.0/20	38.9/18	81.2/32
20) Mid-trigonid crest M_3 + = 1-3	0.0/7	0.0/5	100/6	87.5/8	0.0/16	0.0/19

Table 4: *Trait frequencies for the 20 traits used in this analysis (frequency in percent/n).*

If Upper Paleolithic European dental morphological variation results from admixture between Neandertals and early modern humans we may expect to find that they exhibit trait frequencies that are intermediate between these two 'parental' groups. This is true for only 6 of the 20 dental traits in Table 4 (I^1 Shoveling, C̲ Bushman Canine, M^1 Cusp 5, P_4 Transverse crest, M_1 Deflecting wrinkle, M_1 Cusp 6). In all but one case (M_1 Deflecting wrinkle) the Upper Paleolithic European frequency is closer to that of early modern humans than late Neandertals. This study also indicates that the late Neandertal sample is less divergent (MMD distance is smaller) from modern humans than is the early Neandertal sample. Is this sufficient evidence for significant admixture between the two groups? Certainly it does not disprove it.

On the other hand, none of the unique trait combinations noted earlier (e.g., on the incisors, P_4 and M^1) have been observed in any modern human group, which is compelling evidence to the contrary. Moreover, the fact that the late Neandertal sample is also less divergent from (having a smaller MMD distance) the *Homo erectus* sample than is the early Neandertal sample suggests that while it may be less 'specialized', it is not necessarily more 'modern'. In my view, the reduction in MMD values from earlier to late Neandertal samples is overshadowed by the fact that biological distance between the late Neandertal sample and the Upper Paleolithic European sample, occupying the same geographic area, has been found to be two to three times greater than that of two contemporary human populations separated by large geographic distances (Bailey 2002b). Therefore the slight decrease in MMD values between Neandertals and other groups seems less compelling than the very large and significant MMD values retained in the late Neandertal sample. If the two groups interbred when they met, the interactions were insufficient to significantly affect later human dental morphology.

As regards the species question, there is good evidence that the Neandertal dental pattern has been evolving for a long time, as some of the unique combinations of Neandertal traits are found in low frequencies in their probable ancestors represented at Arago (Bailey 2002 b) and Sima de los Huesos (Martinón-Torres et al. 2006). Moreover, the likelihood that some of these traits are derived in Neandertals (Bailey 2004a; Bailey and Lynch 2005) suggests that when combined with other cranial data (e.g., Harvati 2003, 2004), a good case can be made for Neandertals having distinct specific status. Further study on additional early Upper Paleolithic samples, especially if they can be divided into finer temporal groups (e.g., earlier and later Upper Paleolithic) may help clarify the relationship between and interactions among Neandertals and modern humans.

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