

Modern Human Origins: Midfacial Prognathism, 3D Approach

Hamed Vahdati Nasab
Tarbiat Modares University

Geoffrey A. Clark
Arizona State University

Received: April, 26, 2014 Accepted: June, 01, 2014

Abstract: Neanderthals exhibit a unique midfacial morphology that distinguishes them from their non-Neanderthal contemporaries and from the generalized hominid face. Neanderthal zygomatic and maxillary regions are more sagittally oriented than those of modern people, so the midface projects in a manner, and to an extent, not found in modern humans. This is known as midfacial prognathism (MFP). A decrease in the expression of MFP is a significant point of distinction between Neanderthals and modern humans, and some consider it an important aspect of morphological 'modernity' in general. This research assesses the degree of resemblance in the midfacial region of Upper Pleistocene European hominids including Neanderthals and Upper Paleolithic people. To assess the degree of midfacial resemblance, a new method called Geometric Morphometric 3-Dimensional Analysis (GM3DA) is developed. A computer program transforms morphological raw data into comparable curves that can be analyzed statistically to assess the degree of similarity and difference in the midfaces of different hominids. Using these methods, the results indicate a clear morphological difference in the midfacial region when Neanderthals are compared with Upper Paleolithic Europeans. The results suggest that European Neanderthals constitute a distinct morphological population, at least so far as the midface is concerned.

Keywords: geometric morphometric 3D analysis, Neanderthal, midfacial prognathism, Europe, Upper Pleistocene hominids

Introduction

Facial morphology has played a prominent role in studies of human evolution. The hominid midface is a significant area of study not only because it is important in mastication and associated with sexual selection and social communication, but also because it highlights characters vital to the interpretation of inter- and intraregional variation. The midface is defined as the nasal, maxillary, and zygomatic regions, all of which have been intensively studied.

Neanderthals exhibit a unique facial morphology, midfacial prognathism (MFP) that distinguishes them from their contemporaries, from modern humans, and from the generalized hominid face. Stringer and colleagues (1984: 55) break down MFP into four components: (1) low subspinale angle ($< 115^\circ$), (2) dentition positioned anteriorly (retromolar spaces common, mental foramen usually under M1), (3) low nasiofrontal angle ($< 141^\circ$) and (4) large difference between M1 alveolus and zygomaxillare radii (> 18 mm). However, these supposed autapomorphies have not fared very well over the past quarter century (see Trinkaus [2006] for a current evaluation). Many of them show considerable variation within the Neanderthals themselves and, some would argue, a continuous distribution from the Mousterian to the

early Upper Paleolithic (Frayer 1992, Wolpoff *et al.* 2004, Soficaru *et al.* 2007). Whatever the case, the result is a face that is 'pulled forward' along the midline in a configuration rare or absent in modern humans, although found in some of the Sima de los Huesos specimens (e.g., SH 5) generally thought to represent Neanderthal ancestral populations (Rosas 1997).^{*}Midfacial prognathism is regarded by many workers as an important Neanderthal autapomorphy (e.g., Hublin 1998, Lieberman 1995, Rak 1986, 1993; Rightmire 1997, Smith 1991, Smith *et al.* 2005, Stringer *et al.* 1984, Stringer 1985, Trinkaus 1995).

Hamed Vahdati Nasab
Department of Archaeology
Tarbiat Modares University
Tehran, IRAN
Email: Vahdati@modares.ac.ir
Correspondent Author

Geoffrey A. Clark
School of Human Evolution & Social Change
Arizona State University
Tempe AZ 85287-2402 USA
Email: Geoffrey.Clark@asu.edu

A decrease in the expression of MFP is a significant difference between Neanderthals and modern humans, and is almost certainly due to a corresponding reduction in the size of the anterior dentition and its support structures. Reduction in this feature has been considered by some to be one of the most important aspects of modern morphology (e.g., Rosas and Bastir 2004). We investigate here whether or not, and to what extent, morphological similarity exists in the midfacial region of European Neanderthals and European Upper Paleolithic (EUP) samples generally regarded as *H. sapiens sapiens*. Bräuer and colleagues (2006) suggest that, with regard to the midface, (esp. zygomaxillary angles), early modern Europeans (e.g., Mladeč 1, 2) show significant divergence from both 'early' and 'late' European Neanderthals. However, both Wolpoff *et al.* (2004) and Smith *et al.* (2005) argue that other EUP specimens (esp. Mladeč 5, 6, and 8 – all males) deviate relatively little from European Neanderthals, and relatively more from early Levantine moderns from Qafzeh and Skhul.

Interpretations of the significance of variation in the Neanderthal midface can be reduced to one null and one alternative hypothesis. The null hypothesis (H_0) states that there are no statistically significant morphological differences in the overall form of the midface in Neanderthals and EUP humans from western Eurasia. By itself, the midface cannot be used to discriminate amongst hominid groups in the region. The alternative hypothesis (H_1) states that there is a statistically demonstrable morphological difference in the overall form of the midface when west Eurasian Neanderthals and EUP humans are compared. If adequately characterized, the midfacial region in the existing hominid samples can potentially be used to discriminate amongst west Eurasian Upper Pleistocene hominids.

Methods and Materials

Although computerized statistical methods are used increasingly to study the shape of the hominid cranium (e.g., Harvati 2003a, 2003b; Zollikofer 2002, Zollikofer *et al.* 1995, 1998), the midfacial region has not yet been systematically investigated using three-dimensional techniques specifically designed to capture the complexities of irregular surfaces. In order to conduct this research, a combination of landmark and outline techniques, followed by Procrustes Analysis (Bookstein *et al.* 1999), is used to quantify the outcomes. A new method, Geometric Morphometric Three-Dimensional Analysis (GM3DA), is developed and applied to the surficial midface (Vahdati Nasab and Karnick 2003). Three-dimensional facial data are collected from the midface of modern humans and fossil hominids. A computer program (Karnick 2004) transforms these data into comparable curves to investigate the degree

of similarity and difference between the complex surfaces of the hominid midface.

Data were collected from the right side of the face using a Laser Digitizing Ink (LDI) portable scanner. When the right side of the face was not preserved, or was otherwise unavailable, data from the left side were mirror-imaged and fed into the algorithm. Four strategically-placed, generally-recognized anatomical landmarks were selected on each scanned specimen. These are (1) the deepest part of jugale, (2) the infraorbital foramen, (3) rhinion, and (4) prosthion (Figure 1).

Each scanned face contains thousands of three-dimensional points. Developed for the Institute of Human Origins (IHO) at Arizona State University by researchers at the Partnership for Research in Spatial Modeling (PRISM/ASU), the newly developed software connects each point with its two nearest neighbors, transforming the entire selected surface area into thousands of triangles. To generate a curve between each pair of points, the centers of the triangles are connected using a nearest neighbor algorithm that measures the distance between them. The end result is three curves defined through these points (Figure 1). The curves precisely define the facial morphology between any two reference points. The data captured by the curves represent the actual three-dimensional morphology between each pair of points.

Curve 1 (zygomatic curve) extends from the deepest point of jugale to the infraorbital foramen; it describes the shape of the zygomatic region of the face. Curve 2 (nasal curve) extends from the infraorbital foramen to rhinion; it gives the shape of the nasal area. Curve 3 (maxillary curve) extends from the infraorbital foramen to prosthion; it produces a 3-D section through the maxillary part of the midface. The basic assumption is that, among different hominid taxa, those taxa with similar midfacial morphologies will produce similar curves. GM3DA measures the goodness of fit between two or more different curves and provides a statistical assessment of the degree of similarity and difference.

The goodness of fit between two curves is calculated by:

$$MSE(\phi) = \frac{1}{n} \sum_{i=1}^n (dist(\hat{c}_i, c_i))^2$$

where MSE is the Mean Squared Error, which represents the area between two curves, and n is the number of points to be compared on each curve (50, in this case). The points in curve 1 are denoted by c_i , those on curve 2 by \hat{c}_i . MSE was calculated both with and without rotation of the curves (MSEWR, MSEWOR respectively). To compare each pair of curves, they must first be normalized through rescaling (Dean *et al.* 1996). After each superimposition of the facial curves, the two-dimensional matrix of MSE terms is calculated. The MSE should be small if the two curves pertain to the same taxon (e.g., two modern humans)

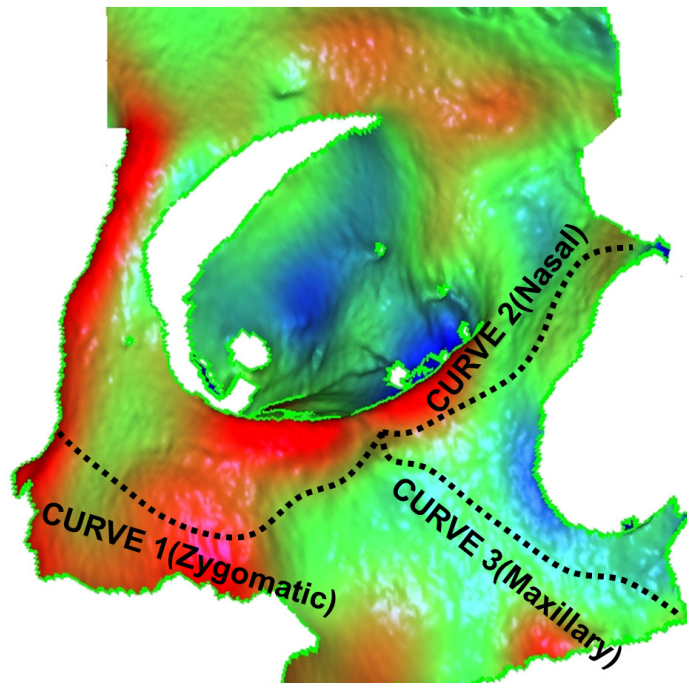


Fig. 1. The zygomatic, nasal, and maxillary curves defined through the facial landmarks. 1 = jugale, 2 = infraorbital foramen, 3 = rhinion, 4 = prosthion.

and relatively large if they do not (e.g., modern human, Neanderthal).

The final stage of analysis is performed after refining the samples using multidimensional scaling (MDS) of the distance matrix (Johnson and Wichern 1988: 572-8, Statistica 6.1 2003). MDS moves objects around in the space defined by the requested number of dimensions (in this case, two) and checks how well the distances between objects can be reproduced by the new configuration. MDS also computes the stress value, used to determine how well (or poorly) a particular configuration reproduces the observed distance matrix. The smaller the stress value, the better the fit of the reproduced distance matrix to that of the observed distance. The stress value transformation essentially creates a 1-dimensional matrix out of a 2-dimensional matrix in order to express and explore relationships in terms of a linear model (Kruskal and Wish 1978).

MDS is sensitive to the range of sample variation and can produce different results with different groups of datasets. In order to normalize the sample variance, a 3-group model (fossil hominids, Eurasians, all samples combined) was prepared for the analysis. In each case MSE was calculated with (MSEWR) and without (MSEWOR) rotation.

The hominid fossils¹ examined come from Middle and

Upper Pleistocene sites in Europe, Asia, and Africa. A few specimens were from Middle Paleolithic archaeological contexts in the Levant. The study collections of *Archaic Homo sapiens* (AHS), Neanderthals, anatomically early modern humans (AMH), and European Upper Paleolithic and Holocene *Homo sapiens* are listed in table 1. Comparative material includes the modern human collections at Arizona State University, and modern Europeans housed at the American Museum of Natural History (AMNH) in New York.

Results

After calculating a 1-dimensional matrix, data were sorted in ascending order based on their linkage distances. The next step filtered the data according to taxon differences. In each case the specimens with the minimum and maximum values were eliminated to avoid distortion caused by outliers. The final step generated a misclassification table expressed as relative frequencies (i.e., percentage of taxon A misclassified as taxon B). This statistic is called the Percentage of Overlap (PO) between A and B. Given that the MSE was calculated with and without rotation, and that there are three sample groups (fossil hominids, Eurasians, and all samples combined), there are six possible POs. Therefore, the Average Percentage of Overlap (APO) was created to summarize overall differences and similarities between each pair of taxa. The APOs for each of the three facial curves are given in TABLES 2-4.

1. High quality epoxy casts at the American Museum of Natural History and Institute of Human Origins were used because access to the originals was not possible for this research

Discussion

Zygomatic Region

It is expected that MFP would be evident in the zygomatic and maxilla, and that the morphology of these areas would be quite distinctive in Neanderthals and modern humans. Curve 1 (deepest part of jugale to infraorbital foramen) encompasses all of the zygomatic bone. Moreover, the zygomatic bone is clearly Neanderthal in overall morphology. Results obtained from comparing the zygomatic region of the samples confirm this assertion (TABLE 2). The data indicate that modern Europeans (ME) and European Neanderthals (EN) exhibit little similarity in their zygomatic morphology (APO: 15%). A comparison of ME with West Asian Neanderthals (WAN) shows even less (APO: 8%).

The data also imply that European Upper Paleolithic (EUP) people have a different zygomatic morphology than European Neanderthals (EN); the degree of similarity between these two groups is relatively low (APO: 30%) compared to the ME/EUP comparison (APO: 79%). The difference is even more obvious when it comes to comparing the EUP with the WAN (APO: 15%). These results indicate that European Upper Paleolithic zygomatic morphology is different from that of European Neanderthals, and resembles that of contemporary modern Europeans.

To the extent that early modern populations are contemporary (or contemporary within the limits of the methods used to date them), they are also most similar in the zygomatic region across space. European Upper Paleolithic specimens most closely resemble the early West Asian moderns from Qafzeh and Skhul (WAHS), well dated to c. 120-80 kya (Klein 1999: 432), and the (somewhat later) South East Asian Upper Paleolithic (SEAUP) specimens (APO: 90%, 83% respectively). Taken at face value, this affinity is even greater than that between the Modern European and European Upper Paleolithic samples. However, the SEAUP specimens are very poorly dated and some (e.g., Liujiang, Wadjak) might actually pertain to the terminal Pleistocene or even the Holocene (Wolpoff 1997: 710, 719, 720).

Nasal Region

Many of the more dramatic features of Neanderthal faces center on the nasal region, leading Wolpoff to observe that "a fully fleshed Neanderthal nose must have been a phenomenal sight" (1997: 660). Curve 2 data monitor the shape of this part of the midface (infraorbital foramen to rhinion). They also suggest that Neanderthal and modern European noses are quite distinct (TABLE 3). However, this relatively low index of similarity (APO: 38%) is not as low as that of the zygomatic region (APO: 15%). Moreover, as with the analysis of the zygomatic, the relative degree of similarity for nasal morphology curves in

modern Europeans and West Asian Neanderthals is lower (APO: 25%) than that of modern Europeans and European Neanderthals (APO: 38%).

Nasal bone surface morphology also seems to show an appreciable difference between European Neanderthals and European Upper Paleolithic humans (APO: 32%). The degree of similarity between these two groups is very similar to that of modern Europeans and European Neanderthals (APO: 38%).

As was the case for the zygomatic region, the nasal bone comparisons among different modern human populations correlate more or less directly with their geographical and temporal distributions. West Asian early moderns most closely resemble the European Upper Paleolithic sample (APO: 83%), closely followed by Southeast Asian Upper Paleolithic humans (APO: 81%). The degree of similarity between contemporary and early modern Europeans is high as well (APO: 77%). This could be taken to indicate more similarity between EUP and ME, and less resemblance between EUP and European Neanderthals.

Maxillary Region

Curve 3 assesses the shape of the maxillary and alveolar regions (Table 4). The ME/EN comparison indicates dissimilar configurations (APO: 29%), but European and West Asian Neanderthals are even more distinct (APO: 15%).

When the European Upper Paleolithic sample is compared to European Neanderthals, there is a moderate degree of resemblance (APO: 53%). To the extent that it is possible to partition the physics of growth fields, as we have done here, a possible explanation for this resemblance, aside from alveolar prognathism itself, could be the reduced effect of MFP on this region.

The basic assumption of this analysis has been that similar morphological regions should produce comparably high APO values throughout the process of measuring the degree of overlap between them. Data for the maxilla are consistent with this statement. As expected, modern and Upper Paleolithic Europeans show one of the highest degrees of similarity for this part of the midface (APO =74%). Modern populations who lived at approximately the same time also appear to represent a high degree of similarity in their facial morphologies, regardless of the geographical distances involved. For example, the APO values for the EUP for both Southeast (SEAUP) and West Asia (WAHS) comparisons are very high (both 83%).

Summary and conclusions

Average percentage of overlap (APO) for all three curves and a summary statistic, grand mean overlap by pairwise comparison, are given in table 5.

Two Kruskal-Wallis tests (1-way ANOVA) were run on

Table 1. List of Specimens.

Name	Abbreviation	Geographical Location	Location	Number
Contemporary Modern Humans				
Australian Aborigines	AB	Australia	AMNH	10
Greeks	GK	Europe	AMNH	10
Germans	GE	Europe	AMNH	5
Austrians	AUS	Europe	AMNH	5
Hungarians	HUG	Europe	AMNH	9
Scandinavians	SCA	Europe	AMNH	5
Eskimos	ESK	Alaska	AMNH	8
South East Asians	SEA	Asia	AMNH	10
Africans (Nubians)	NUB	Africa	ASU	10
Total				72
Archaic Homo sapiens				
Petalona I	EAHS	Greece	AMNH	
Arago XXI	EAHS	France	AMNH	
Steinheim I	EAHS	Germany	AMNH	
Sima de los Huesos	EAHS	Spain	AMNH	
Bodo	AFAHS	Ethiopia	AMNH	
Broken Hill I	AFAHS	Zimbabwe	AMNH	
Dali	AAHS	India	AMNH	
Total				7
Homo neanderthalensis				
La Ferrassie I	EN	France	AMNH	
La Ferrassie I (reconstr'd)	EN	France	AMNH	
St. Césaire	EN	France	AMNH	
La Chapelle-aux-Saints	EN	France	AMNH	
La Quina H18	EN	France	AMNH	
Le Moustier I	EN	France	AMNH	
Gibraltar	EN	Gibraltar	AMNH	
Guattari	EN	Italy	AMNH	
Saccopastore I	EN	Italy	AMNH	
Krapina C	EN	Croatia	AMNH	
Amud I	WAN	Levant	AMNH	
Amud I	WAN	Levant	IHO	
Shanidar I	WAN	Iraq	AMNH	
Shanidar V	WAN	Iraq	AMNH	
Teshik Tash	WAN	Uzbekistan	IHO	
Total				15
Upper Paleolithic Modern Humans				
Grimaldi	EUP	Italy	AMNH	
Furfooz I	EUP	Belgium	AMNH	
Furfooz II	EUP	Belgium	AMNH	
Oberkassel I	EUP	Germany	AMNH	
Oberkassel II	EUP	Germany	AMNH	
Cro-Magnon I	EUP	France	AMNH	
Cro-Magnon II	EUP	France	AMNH	
Predmost IV	EUP	Czech Republic	AMNH	
Predmost III	EUP	Czech Republic	AMNH	
Brunn III	EUP	Czech Republic	AMNH	
Unknown	EUP	Unknown	AMNH	
Unknown	EUP	Unknown	AMNH	
Wadjak I	SEAUP	Indonesia	AMNH	
Liujiang I	SEAUP	China	AMNH	
Talgai	SEAUP	Australia	AMNH	
Truganini	SEAUP	Indonesia	AMNH	
Okinawa	SEAUP	Japan	AMNH	
Unknown	SEAUP	Tasmania	AMNH	
Total				18

Early Anatomically Modern Humans

Florisbad I	AFHS	South Africa	AMNH
Jebel Irhoud I	AFHS	Morocco	IHO
Skhul V	WAHS	Levant	AMNH
Skhul IV	WAHS	Levant	AMNH
Qafzeh VI	WAHS	Levant	AMNH
Qafzeh IX	WAHS	Levant	IHO
Qafzeh XI	WAHS	Levant	IHO
Total			

7

Holocene Modern Humans

Sclayn	EHO	Belgium	AMNH
Offnet	EHO	Germany	AMNH
Unknown	EHO	Europe	AMNH
Unknown	EHO	Europe	AMNH

4

Grand Total:

123

the data summarized in Table 5 (Siegel 1956: 184-194). The first sought to assess the effect that the combined Neanderthal/AHS sample had on all the bivariate comparisons that included these taxa; the second tried to determine whether or not there are any statistically-significant differences between the combined Neanderthal sample (EN + WAN) and AHS. With $\alpha = .01$ or less, the null hypothesis (H_0) was rejected in both cases ($p(\alpha) = .001, .007$ respectively). The combined Neanderthal/AHS samples are distinct so far as the midface is concerned; there is also a significant difference between Neanderthals and *Archaic Homo sapiens*, albeit one that approaches the level of significance.

In sum, the APOs and their grand means, and the Kruskal-Wallis test, are relatively consistent in showing little resemblance between Neanderthals and modern humans and, in both cases, a high degree of intragroup similarity. More specifically, (1) modern Europeans (ME) differ markedly from both Neanderthal groups, with APO grand means of 16% (WAN) and 27% (EN) respectively. (2) West Asian and European Neanderthal midfaces express a relatively high degree of similarity (62% overlap). (3) The two Upper Paleolithic samples (EUP, SEAUP) tend to resemble one another (82%), modern Europeans (77%) and West Asian *Archaic Homo sapiens* (85%). (4) European Neanderthals and European Upper Paleolithic samples express only a moderate degree of similarity (39%), about the same as (5) modern Europeans and Southeast Asian Upper Paleolithic groups (42%). Finally, (6) West Asian Neanderthals and the European Upper Paleolithic people are quite dissimilar from one another (only 22% overlap). In all three curves, specimens assigned to the Upper Paleolithic exhibit the highest degree of morphological similarity, regardless of geographical provenience.

These results could be interpreted in two ways. As they are not mutually exclusive, a third possibility is a combination of both of them (e.g., Smith's Assimilation Model [Smith

et al. 2005: 15]). On the one hand, the results are consistent with the relatively recent, relatively rapid spread of modern humans from a geographical origin somewhere in East Africa proposed by advocates of the Recent African Origin (RAO) model (e.g., Stringer 1992, Bräuer 1992). Most of the support for the RAO model does not come from the archaeology or the human paleontology, however, but rather from biomolecular research that indicates a human migration or range extension out of Africa over some interval between 100 and 50 kya (Willoughby 2006: 127-160). Since there is no genetic yardstick with which to determine species differences, the genes remain silent on the issue of whether the African excursion was by a new species, or by a subspecies of an old one (Clark 1999).

On the other hand, the results could represent a general time trend in the expression of mid-facial prognathism that cross-cuts the analytical units adopted here, a consequence of a relaxation of the selective forces that would favored retention of a robust anterior dentition and its support structures in the mandible and maxilla. This trend would have a 'patchy' or mosaic expression in time and space, consistent with the mosaic pattern in human adaptation documented in Europe by the archaeological record of both the Middle and Upper Paleolithic (e.g., Straus 2003, Clark 2007). Since adaptation is a regional phenomenon regardless of who is doing the adapting, vectored change in the expression of MFP could be explained by increasing reliance upon technology (e.g., fire, more efficient lithic technologies, mass hunting techniques, the appearance of multi-component tools and weapons, etc.) and by changes in social organization (e.g., changes in local group size and composition, aggregation and dispersal patterns at different temporal scales, differences in mobility, more extensive mating networks, lithic procurement strategies, etc.) over the course of the Upper Pleistocene (e.g., Clark 1992, Wolpoff *et al.* 2004). It might simply be the case that paramasticatory use of the anterior dentition

Table 2. Percentage of Overlap among the Samples for the Zygomatic Curve.
(ME: Modern European, EN: European Neanderthal, EUP: European Upper Paleolithic, WAN: West Asian Neanderthal, WAHS: West Asian Homo sapiens, SEAUP: South East Asian Upper Paleolithic).

Data Sets	Fossil Hominids		Eurasians		All Combined		Mean
	MSEWOR	MSEWR	MSEWOR	MSEWR	MSEWOR	MSEWR	
ME-EN	N/A	N/A	0	0.09	0.44	0.09	0.15
EUP-EN	0.42	0.25	0.25	0.25	0.50	0.17	0.31
WAN-EN	0.60	1.00	0.60	1.00	0.60	0.80	0.77
ME-EUP	N/A	N/A	0.52	0.78	0.96	0.91	0.79
EUP-WAN	0.42	0	0.17	0	0.33	0.17	0.18
WAHS-EUP	1.00	0.60	1.00	1.00	0.80	1.00	0.90
SEAUP-EUP	0.83	0.67	1.00	0.83	0.83	0.83	0.83
ME-SEAUP	N/A	N/A	0.70	0.35	0.74	0.35	0.53
ME-WAN	N/A	N/A	0.09	0	0.22	0	0.08

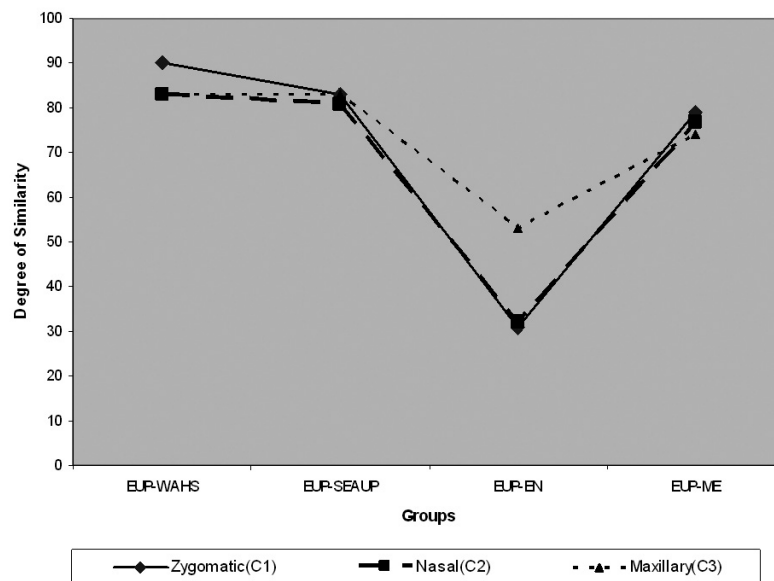


Fig. 2. Bivariate comparisons between EUP and other samples displaying the absence of consistent pattern in the three components of the midface.

persisted longer in mid-latitude Eurasia than it did in more southerly locales and that selective pressure that favored its phenotypic expression was relaxed relatively quickly because of the introduction and/or emergence of relatively rapid technological changes – changes we typically associate with textbook descriptions of the Upper Paleolithic. At present, we lack the temporal and spatial resolution to be able to choose between these two alternatives.

If the degree of difference characteristic of the comparison between Neanderthals and early modern populations in Europe can be generalized, then the EN/EUP comparison should be relatively similar to the analogous comparisons in other geographical areas (i.e., EUP/WAHS, EUP/

SEAUP, EUP/ME). However, the results do not support this assumption and suggest that the EN/EUP gradient is not consistent with the relationship to the other groups (Figure 2).

Although the differences in the EN/EUP comparison are not as great as those in the EN/ME comparison, the midfacial morphologies are, nevertheless, quite distinct. There is no statistically demonstrable morphological resemblance between European Neanderthals and early modern Europeans. Therefore, H_0 is rejected, and H_1 is accepted: there is a statistically demonstrable morphological difference in the overall form of the midface when west Eurasian Neanderthals and EUP humans are compared.

These results also suggest that (1) there is no evidence

Table 3. Percentage of Overlap among the Samples for the Nasal Curve.

Data Sets	Fossil Hominids		Eurasians		All Combined		
Methods	MSEWOR	MSEWR	MSEWOR	MSEWR	MSEWOR	MSEWR	Mean
ME-EN	N/A	N/A	0.43	0.09	0.48	0.52	0.38
EUP-EN	0.33	0.25	0.42	0.25	0.25	0.42	0.32
WAN-EN	0.20	0.40	0.20	0.40	0.80	0.60	0.43
ME-EUP	N/A	N/A	0.74	0.83	0.70	0.83	0.77
EUP-WAN	0.33	0.08	0.42	0.17	0	0.33	0.22
WAHS-EUP	1.00	1.00	0.60	0.80	1	0.60	0.83
SEAUP-EUP	0.67	1.00	0.67	0.83	0.83	0.83	0.81
ME-SEAUP	N/A	N/A	0.30	0.43	0.43	0.42	0.40
ME-WAN	N/A	N/A	0.48	0.09	0.13	0.30	0.25

Table 4. Percentage of Overlap among the Samples for the Maxillary Curve.

Data Sets	Fossil Hominids		Eurasians		All Combined		
Methods	MSEWOR	MSEWR	MSEWOR	MSEWR	MSEWOR	MSEWR	Mean
ME-EN	N/A	N/A	0.43	0.09	0.48	0.52	0.38
EUP-EN	0.33	0.25	0.42	0.25	0.25	0.42	0.32
WAN-EN	0.20	0.40	0.20	0.40	0.80	0.60	0.43
ME-EUP	N/A	N/A	0.74	0.83	0.70	0.83	0.77
EUP-WAN	0.33	0.08	0.42	0.17	0	0.33	0.22
WAHS-EUP	1.00	1.00	0.60	0.80	1.00	0.60	0.83
SEAUP-EUP	0.67	1.00	0.67	0.83	0.83	0.83	0.81
ME-SEAUP	N/A	N/A	0.30	0.43	0.43	0.42	0.40
ME-WAN	N/A	N/A	0.48	0.09	0.13	0.25	

for a clinal reduction in prognathism from Neanderthals to early modern Europeans (but cf. Wolpoff *et al.* 2004: 531-3). Other workers (esp. Frayer 1992, Frayer *et al.* 2005), however, using different methods and variables, have made a strong case for vectored, although not necessarily gradual or regular, change in the appearance of modern craniofacial morphology, suggesting that these populations were never static nor unidimensional in any of their alleged autapomorphies (Wolpoff *et al.* 2001, 2004). (2) Regardless of the possible evolutionary relationships between Neanderthals and modern humans in Europe, the data indicate different morphologies in the midfaces of these two groups – a conclusion with which practically all MHO researchers would agree. At issue, though, is how much difference makes a difference so far as comparisons with modern humans are concerned. Finally, (3) the outcome of this work tends to call into question the suggestion by Wolpoff and colleagues (2004) that the facial morphology of some early modern Europeans (e.g., Mladeč 5, 6 and 8), including the zygomaxillary angles, does not diverge significantly from that of European Neanderthals. Wolpoff

would disagree, contending that “. . . the Mladeč males have sagittal dimensions and profiles that deviate far less from the Neanderthals than they deviate from the Skhul/Qafzeh males” (2004: 531). Other workers (e.g., Smith 2002, Smith *et al.* 2005) also claim that directional change is evident in some Neanderthal craniofacial features, and that modern-like traits show up in some late Neanderthals (e.g., Vindija, St. Césaire). At present the issue is not resolved.

Epilogue

In what is arguably the best-balanced recent treatment of morphological variation in Upper Pleistocene Homo, Trinkaus (2006) makes the point that it is we, rather than the Neanderthals, who are the ‘more derived’ of the two groups. Although the mechanisms of, and degree of admixture with, late archaic humans are hotly contested, and the time/space distributions of both groups remain to be assessed, gaps in the fossil record; ‘coarse-grained’, low resolution chronologies, and different conceptual

Table 5. Average Percentages of Overlap for all Three Curves.

Comparison	Curve 1 (zygomatic)	Curve 2 (nasal)	Curve 3 (maxillary)	Grand Mean
ME-EN	0.15	0.38	0.29	0.27
EUP-EN	0.31	0.32	0.53	0.39
WAN-EN	0.77	0.43	0.67	0.62
ME-EUP	0.79	0.77	0.74	0.77
EUP-WAN	0.18	0.22	0.26	0.22
WAHS-EUP	0.90	0.83	0.83	0.85
SEAUP-EUP	0.83	0.81	0.83	0.82
ME-SEAUP	0.53	0.40	0.34	0.42
ME-WAN	0.08	0.25	0.15	0.16

frameworks (which, in turn, affect variable choice and measurement criteria) all play a role in these critical epistemological issues (see papers in Clark and Willermet 1997, Clark 1999b, Willermet and Clark 1995, Willermet 2001).

Most workers use as a baseline for comparison a general model for early and middle Pleistocene Homo premised on (1) the emergence of early Homo in east Africa in the late Pliocene (c. 2.5 mya), (2) a subsequent dispersal throughout Africa and mid-latitude Eurasia in the early Pleistocene (c. 1.8 mya), (3) a Middle Pleistocene expansion, or range extension, into the higher latitudes of Eurasia, and the emergence of regional variation in craniofacial and post-cranial morphologies; (4) morphologically distinct regional populations after c. 250 kya (Neanderthals and early modern humans in western Eurasia, east Africa; late archaic humans in central, southern and eastern Asia; northwest Africa), and (5) an expansion of early moderns out of Africa and throughout Eurasia after c. 50 kya that extirpated, out-competed or absorbed various archaic populations (Trinkaus 2006: 598).

Of 75 cranial, mandibular, dental, axial and appendicular traits in which Neanderthals and/or modern humans are derived relative to Early and Middle Pleistocene Homo, c. 25% are shared among Neanderthals and modern humans (i.e., synapomorphic, c. 25% can be argued to be uniquely derived Neanderthal autapomorphies, and the remaining c. 50% are largely confined to modern humans. The results are similar whether the Neanderthals are compared with the earliest modern humans, or whether they are compared with their late Pleistocene descendants. The implication is that the emphasis on Neanderthal distinctiveness is somewhat misplaced, and that increased attention to the evolutionary biology of early and recent modern humans might redress this imbalance (Trinkaus 2006: 597, 604-607).

Acknowledgments

Special thanks to the Catherine B. Reynolds Foundation and Institute of Human Origins at Arizona State University for financial support, and to Donald C. Johanson and William H. Kimbel for scientific and editorial assistance. Pushpak Karnick at the PRISM (Partnership for Research and Spatial Modeling) lab at ASU wrote the computer program required to analyze the data (Karnick 2004). Keith Kintigh (School of Human Evolution and Social Change) offered advice on the appropriate statistical approaches, Matt Tocheri helped with the 3D modeling software, and Diane Hawkey (SHESC), Ian Tattersall, Ken Mowbray and Gary Sawyer (AMNH) graciously allowed access to the relevant collections.

Endnote

*. Over the past 23 years, many of Stringer's claimed autapomorphies have been questioned by other workers (e.g., Franciscus and Trinkaus, 1995; Frayer, 1992) or shown to have frequencies $\leq 50\%$ in specimens where the relevant anatomical parts are preserved (Wolpoff and Frayer 2004).

References

- Bookstein, F., K. Schafer, H. Prossinger, H. Seidler, M. Fielder, C. Stringer, G.W. Weber, J. Arsuaga, D. Slice, J. Rohlf, W. Recheis, A. Mariam, L. Marcus,
1999 Comparing frontal cranial profiles in archaic and modern Homo by morphometric analysis. *The Anatomical Record* 257, 217-224.
- Bräuer, G.,
1992 Africa's place in the evolution of Homo sapiens. In: Bräuer, G & Smith, F. (Eds.), *Continuity or Replacement: Controversies in Homo sapiens Evolution*. Balkema, Rotterdam, pp.83-98.
- Bräuer, G. and H. Broeg,
1998 On the degree of Neanderthal-modern continuity in the earliest Upper Paleolithic crania from the Czech Republic: evidence from non-

- metrical features. In: Omoto, K & Tobias, P. (Eds.), *The Origins of Past Modern Humans: Toward Reconciliation*. World Scientific, Singapore, pp.106-125.
- Bräuer, G., H. Broeg and C.B. Stringer,
2006 The earliest Upper Paleolithic crania from the Czech Republic and the question of Neanderthal-modern continuity: material evidence from the fronto-facial region. In: Havarti, K. & Harrison, T. (Eds.), *Neanderthals Revisited – New Approaches and Perspectives*. Springer, Heidelberg, pp.280-296.
- Clark, G. A.,
1999a Neanderthal genetics. *Science* 277, 1024- 1025.
1999b Modern human origins – highly visible, curiously intangible. *Science* 283, 2029-2032; 284, 917.
2007 Putting transitional research in a broader context. In: Riel-Salvatore, J. & Clark, G.A. (Eds.), *New Approaches to the Study of the Early Upper Paleolithic ‘Transitional’ Industries of Western Eurasia: Transitions Great and Small*. Pp.143-178, Archaeopress, BAR International Series No. 1620, Oxford.
- Dean, D., F. L. Marcus, F. Bookstein,
1996 Chi-square test of biological space curve affinities. In: Marcus, L.F., Conti, M., Loy, A., Naylor, G. J. P. & Slice, D. (Eds.), *Advances in Morphometrics*. Plenum, New York, pp.235-251
- Franciscus, R. G. and E. Trinkaus,
1995 Determinants of retromolar space presence in Pleistocene Homo mandibles. *Journal of Human Evolution* 28, 577-595.
- Frayer, D.,
1992 The presence of Neanderthal features in post-Neanderthal Europeans. In: Bräuer, G & Smith, F.(Eds.), *Continuity or Replacement: Controversies in Homo sapiens Evolution*. Balkema, Rotterdam, pp. 179-188.
- Frayer, D., M. Wolpoff, A. Thorne, F. Smith, G. Pope,
1993 Theories of modern human origins: the paleoanthropological test. *American Anthropologist* 95, 14-50.
- Harvati, K.,
2003a The Neanderthal taxonomic position: models of intra- and interspecific craniofacial variation. *Journal of Human Evolution* 44, 107-132.
2003b Quantitative analysis of Neanderthal temporal bone morphology using three-dimensional geometric morphometrics. *American Journal of Physical Anthropology* 120, 323-338.
- Hawks, J.,
2004 How much can cladistics tells us about early hominid relationships? *American Journal of Physical Anthropology* 125, 207-219.
- Hublin, J. J.,
1998 Climatic changes, paleogeography and the evolution of the Neanderthals. In: Akazawa,T., Aoki, K & Bar-Yosef, O.(Eds.), *Neanderthal and Modern Humans in Western Asia*. Plenum, New York, pp. 295-310.
- Johnson, R. A. and D. W. Wichern,
1988 *Applied Multivariate Statistics* (2nd edition, revised). Englewood Cliffs, Prentice-Hall, NJ.
- Karnick, P.,
2004 *Geometric Morphometric 3-Dimensional Analysis (GM3DA)*. Partnership for Research in Spatial Modeling (PRISM), Arizona State University.
- Klein, R. G.,
1999 *The Human Career* (2nd edition, revised). University of Chicago Press, Chicago.
- Kruskal, J. B. and M. Wish,
1978 *Multidimensional Scaling*. Beverly Hills: Sage Publications, Inc., Quantitative Applications in the Social Sciences No. 11.
- Lieberman, D.,
1995 Testing hypotheses about recent human evolution from skulls. *Current Anthropology* 36, 159-197.
- Rak, Y.,
1986 The Neanderthal: a new look at an old face. *Journal of Human Evolution* 15, 151-164.
1993 Morphological variation in Homo neanderthalensis and Homo sapiens in the Levant, a biogeographic model. *Journal of Human Evolution* 20, 283-290.
- Rightmire, P.,
1997 Deep roots for the Neanderthals. *Nature* 389, 917-918.
- Rosas, A. and M. Bastir,
2004 Geometric morphometric analysis of allometric variation in the mandibular morphology of the hominids of Atapuerca, Sima de los Huesos site. *The Anatomical Record Part A*, 278A, 551-560.
- Rosas, A.,
1997 A gradient of size and shape for the Atapuerca sample and Middle Pleistocene hominid variability. *Journal of Human Evolution* 33, 319-331.
- Siegel, S.,
1956 *Non-Parametric Statistics*. McGraw-Hill, New York.
- Smith, F. H.,
1991 The Neanderthals: evolutionary dead ends or ancestors of modern people? *Journal of Anthropological Research* 47, 219-238.
2002 Migrations, radiations and continuity: patterns in the evolution of Middle and Late Pleistocene humans. In: Hartwig, W. (Ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp.437-456.
- Smith, F. H., I. Janković, I. Karavanic,
2005 The assimilation model, modern human origins in Europe, and the extinction of Neanderthals. *Quaternary International* 137, 7-19.
- Soficaru, A., C. Petrea, A. Dobos, E. Trinkaus,
2007 The human cranium from Pestera Cioclivina Uscata, Romania. *Current Anthropology* 48, 611-619.
- Statistica Version 6.1 Data Analysis Software System 2007. Tulsa: StatSoft, Inc. www.statsoft.com.
- Straus, L. G.,
2003a On the demise of the Neanderthals. *Quaternary International* 137, 1-67.
2003b The Aurignacian? Some thoughts. In: Zilhão, J. & d’Errico, F.(Eds.), *The Chronology of the Aurignacian and the Transitional Technocomplexes*. Trabalhos de Arqueologia, Lisboa, pp. 11-17.
- Stringer, C. B.,
1985 Middle Pleistocene hominid variability and the origin of Late Pleistocene humans. In: Delson, D.(Ed.), *Ancestors: the Hard Evidence*. Alan Liss. New York, pp.289-295.
1992 Replacement, continuity and the origin of Homo sapiens.” In: Bräuer, G. & Smith, F.(Eds.), *Continuity or Replacement: Controversies in Homo sapiens Evolution*. Balkema, Rotterdam, pp.9-24.
- Stringer, C. B., J. J. Hublin, B. Vandermeersch,
1984 The origin of anatomically modern humans in Western Europe.” In: Smith, F.H. & Spencer, F.(Eds.), *The Origins of Modern Humans*. Alan Liss, New York, pp. 51-135.
- Trinkaus, E.,
1995 Testing hypothesis about recent human evolution from skulls. *Current Anthropology* 36, 185-186.
2006 Modern human versus Neanderthal distinctiveness. *Current Anthropology* 47, 597-620.
- Vahdati Nasab, H. and P. Karnick,
2004 *A New Method for the Analysis of Complex Surfaces: Geometric Morphometric 3-Dimensional Analysis (GM3DA)*. Partnership for Research in Spatial Modeling and the Institute of Human Origins, Arizona State University.
- Willermet, C. M.,
2001 *Fuzzy Logic as a Classification Tool: a Case Study*

- Using *Levantine Archaic Hominids*. Ph.D dissertation, Department of Anthropology, Arizona State University. Ann Arbor, University Microfilms, Inc, MI.
- Willermet, C. M. and G. A. Clark,
1995 Paradigm crisis in modern human origins research. *Journal of Human Evolution* 29, 487-490.
- Willoughby, P.,
2006 *The Evolution of Modern Humans in Africa*. Lanham, MD, AltaMira.
- Wolpoff, M. H.,
1997 *Human Evolution*. McGraw-Hill, New York.
- Wolpoff, M. H. and D. Frayer,
2004 Unique ramus anatomy in Neanderthals? *American Journal of Physical Anthropology* 128, 245-251.
- Wolpoff, M. H., J. D. Hawks, D. Frayer and K. Hunley,
2001 Modern human ancestry at the peripheries: a test of the replacement theory. *Science* 291, 292-297.
- Wolpoff, M. H., B. Mannheim, A. Mann, J. Hawks, R. Caspari, K. Rosenberg, D. Frayer, G. Gill and G. A. Clark,
2004 Why not the Neanderthals? *World Archaeology* 36, 527-546.
- Zollikofer, C. P. E.,
2002 A computational approach to paleoanthropology. *Evolutionary Anthropology Supl.* 1, 64-67.
- Zollikofer, C. P. E., M. S. Ponce de Léon, R. D. Martin, P. Stucki,
1995 Neanderthal computer skulls., *Nature* 375: 283-285.
- Zollikofer, C. P. E., M. S. Ponce de Léon, R. D. Martin,
1998 Computer-assisted paleoanthropology. *Evolutionary Anthropology* 6, 41-54.