



The Neanderthal taxonomic position: models of intra- and inter-specific craniofacial variation

Katerina Harvati

Department of Anthropology, New York University, 25 Waverly Place, New York, NY 10003, USA

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Abstract

The Neanderthal taxonomic position is a matter of wide disagreement among paleoanthropologists. Some workers consider this fossil human group to represent a different species, *Homo neanderthalensis*, while others see it as a subspecies of *Homo sapiens*. This study developed two models of morphological variation to be applied to a comparison between Neanderthals and modern humans: modern human populations provided a measure of intra-specific variation, while the species and subspecies of *Pan* provided measures of both intra- and inter-specific morphological differences. Although such an approach has been advocated strongly, it has not been systematically undertaken until recently. The techniques of geometric morphometrics were used to collect data in the form of three-dimensional coordinates of craniofacial landmarks. The data were processed using generalized procrustes analysis, and analyzed by an array of multivariate statistical methods, including principal components analysis, canonical variates analysis and Mahalanobis D^2 . The morphological distances between Neanderthals and modern humans, and between Neanderthals and Late Paleolithic/early anatomically modern specimens, are consistently greater than the distances among recent human populations, and greater than the distances between the two chimpanzee species. Furthermore, no strong morphological similarities were found between Neanderthals and Late Paleolithic Europeans. This study does not find evidence for Neanderthal contribution to the evolution of modern Europeans. Results are consistent with the recognition of Neanderthals as a distinct species.

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1. Introduction

The taxonomic position of Neanderthals and their role in the evolution of modern Europeans have been at the center of considerable debate in paleoanthropology since the original assignment of Neanderthals to a separate species from living

humans, *Homo neanderthalensis* (King, 1864). This debate continues to the present, and is centered on two main hypotheses of modern human origins, the replacement and the multiregional models.

Proponents of the replacement model of modern human origins consider Neanderthals to have had little or no contribution to the evolution of modern humans, and tend to view this group as a separate species (Stringer et al., 1984; Tattersall,

E-mail address: katerina.harvati@nyu.edu (K. Harvati).

1986; Stringer and Andrews, 1988; Stringer, 1989, 1992; Tattersall, 1992; Stringer, 1994; Tattersall, 2000). They emphasize the great morphological and genetic distance, as well as behavioral differences surmised from the archaeological record, between Neanderthals and modern humans (Stringer, 1974; Cann et al., 1987; Mellars, 1989; Stringer, 1989, 1992; Lahr, 1996; Schwartz and Tattersall, 1996a,b; Harpending and Relethford, 1997; Krings et al., 1997; Turbón et al., 1997; Harpending et al., 1998; Krings et al., 1999, 2000; Ovchinnikov et al., 2000; Pearson, 2000). Supporters of the multiregional model, on the other hand, see Neanderthals as at least partial ancestors of Late Paleolithic and modern Europeans (Wolpoff, 1989, 1992; Wolpoff et al., 1994, 1997; Wolpoff and Caspari, 1997; Wolpoff et al., 2001). These authors emphasize Neanderthal-like features found in some Late Paleolithic European specimens, as well as what they see as trends for modernization in some late Neanderthal samples (Smith, 1982, 1984; Smith et al., 1989; Wolpoff, 1989; Smith, 1992; Wolpoff, 1992; Frayer et al., 1993; Churchill and Smith, 2000; Wolpoff et al., 2001). Several intermediate positions have also been formulated, including replacement with various degrees of gene flow from Neanderthals (Bräuer, 1984, 1989, 1992; Duarte et al., 1999), as well as a subspecific Neanderthal status without contribution to the modern human gene pool (Delson, 1989; Dean et al., 1998).

It is generally agreed that assignment of fossil samples to species taxa should involve analogy to living biological species that are phylogenetically, geographically and ecologically similar to the fossil organisms studied (Delson, 1989; Albrecht and Miller, 1993; Shea et al., 1993; Szalay, 1993). The range of morphological variation within living species must be evaluated, so that a measure of the geographic, sexual and ontogenetic variation to be expected in a fossil sample can be obtained. However, the morphological difference between closely related species must also be assessed when assigning fossil samples to species taxa, as it has been proposed that closely related primate species could not be differentiated on the basis of bony morphology alone (Tattersall, 1986, 1992; Cope, 1993; Kimbel and Rak, 1993; Tattersall, 1993). While

several studies have compared the morphological differences between Neanderthals and modern humans to the intra-specific morphological variation among modern human populations (Stringer, 1974; Howells, 1989; Stringer, 1989; Bräuer and Rimbach, 1990; Stringer, 1992; Turbón et al., 1997; Bräuer and Broeg, 1998; Pearson, 2000), a comparison of these differences to patterns of inter-specific diversity has been neglected.

The present study developed models of variation based on two living taxa, modern humans and chimpanzees, in order to obtain measures of both intra- and inter-specific variation. These measures were applied to a comparison between Neanderthals and modern humans with the purpose of clarifying the taxonomic position of this fossil human group. This study is the first comprehensive attempt to compare degrees of morphological diversity between Neanderthals and modern humans to the morphological variation present both in modern humans and in another living primate taxon. Such an approach has been advocated strongly by several workers (Delson, 1989; Shea et al., 1993), but has not been systematically undertaken until now. Recently, Schillaci and Froelich (2001) compared the inter-specific diversity among macaque species to the morphological differences between Neanderthals and Late Paleolithic Europeans. However, these authors did not develop a measure of intra-specific variation in the macaques, and did not include a comparison of either of these fossil human groups to recent humans.

2. Models and hypotheses

Two models of variation were developed, one based on modern human populations and one based on the two chimpanzee species and two of the subspecies of *Pan troglodytes*. Nine modern human populations were included, spanning the extremes of the modern human geographical range and a time depth back to the Epipaleolithic. Modern humans represent the closest living relatives of the fossil hominins studied, and as such they provide the best model for comparisons to them. However, this model can only provide a measure of intra-specific variation.

A measure of both intra- and inter-specific variation was obtained from the model based on the genus *Pan*. This taxon is often considered to be the closest living relative to humans, and has been used as a model for early fossil hominins (Shea et al., 1993), although it may not represent the most appropriate model ecologically for Pleistocene humans. *Pan* is differentiated into two species, *P. troglodytes* and *P. paniscus*, and *P. troglodytes* is further subdivided into three subspecies, *P. t. verus*, *P. t. schweinfurthii* and *P. t. troglodytes*. The alpha taxonomy of this genus is not completely resolved, as recent genetic evidence from mitochondrial DNA has questioned the number of species and subspecies present in *P. troglodytes* (Morin et al., 1994; Gonder et al., 1997). This study accepts the two commonly recognized species of *Pan* and the three subspecies of *P. troglodytes*. It includes samples from both species and from two subspecies of *P. troglodytes*, *P. t. troglodytes* and *P. t. schweinfurthii*. *P. t. verus*, whose subspecific status has been questioned, was not included.

The measures of morphological distance among modern human populations, as well as between the two chimpanzee species and the two common chimpanzee subspecies, were compared to the morphological distances between Neanderthals and recent human populations and Neanderthals and Late Paleolithic specimens. Two predictive hypotheses were tested based on these two approaches: (A) Neanderthals and modern humans represent two different species, and Neanderthals did not contribute to the evolution of modern Europeans; and (B) Neanderthals and modern humans represent populations of the same species, and Neanderthals contributed to the evolution of modern Europeans. Hypothesis A predicts that Neanderthals would be more distant morphologically from modern human populations than modern human groups are from each other, and more distant than the two common chimpanzee subspecies are from each other. The morphological distances between Neanderthals and modern humans would be approximately as great as, or greater than, that between the two chimpanzee species. Furthermore, the morphological distance between Neanderthals and Late Paleolithic Euro-

peans, as well as recent Europeans, would be as great as the distances between Neanderthals and other modern human populations, and no similarities would be found between the two fossil groups.

Hypothesis B predicts that the morphological distances between Neanderthals and modern humans would be equivalent to the distances among modern human populations, or to that between the two common chimpanzee subspecies. It would be smaller than that present between the two chimpanzee species. The morphological distance between Neanderthals and Late Paleolithic Europeans would be smaller than the distances between Neanderthals and the other modern human groups and the two fossil groups would show morphological similarities. Such a small distance or morphological similarities would not necessarily be found between Neanderthals and recent Europeans, as the similarities between Neanderthals and Late Paleolithic Europeans are expected to be much stronger than those between Neanderthals and recent Europeans if Neanderthals contributed to the modern European gene pool (Relethford, 2001).

3. Materials and methods

3.1. Samples

Two comparative samples of modern human populations and of chimpanzee species and subspecies were included, as well as a sample of Late Pleistocene fossil hominins. The same measurements were collected in all samples and all data were collected by the author.

The modern human comparative sample included nine modern human populations, each consisting of approximately 30 individuals, comprising a total of 266 individuals (Table 1). Following Howells (1973, 1989), these populations were chosen to represent biological populations limited in space and time. When possible, subsamples of Howells' populations were used. The Epipaleolithic material from Afalou and Taforalt, dated to 14–8.5 ka (Lahr, 1996), was merged to represent one population, which was included in order to give a time dimension in the comparative sample.

Table 1

List of specimens by population for the comparative modern human and chimpanzee samples for each step

Group		Step 1	Step 2
Modern humans		246	266
Andamanese ^a	(Andaman Islands, India)	31 (14M, 17F)	34 (15M, 19F)
Australians	(New S. Wales, South Australia)	29 (18M, 11F)	31 (20M, 11F)
Berg ^a	(Austria)	29 (14M, 15F)	29 (14M, 15F)
Dogon ^a	(Mali, West Africa)	31 (13M, 14F)	33 (15M, 18F)
Epipaleolithic	(Morocco and Algeria)	17 (12M, 5F)	28 (18M, 10F)
Inugsuk ^a	(Greenland)	30 (15M, 15F)	30 (15M, 15F)
W. Eurasian	(Egypt, Dalmatia, Greece, Italy)	22 (13M, 8F, 1U)	23 (13M, 9F, 1U)
Khoisan	(South Africa)	29 (15M, 14F)	30 (16M, 14F)
Tolai ^a	(New Britain, Melanesia)	28 (13M, 15F)	28 (13M, 15F)
Chimpanzees		91	92
<i>Pan paniscus</i>	(Zaire)	34 (16M, 19F)	34 (16M, 19F)
<i>Pan t. schweinfurthii</i>	(Zaire)	29 (18M, 11F)	30 (18M, 12F)
<i>Pan t. troglodytes</i>	(Zaire, Cameroon)	28 (18M, 9F, 2U)	28 (18M, 9F, 2U)

The sex composition of the samples is indicated in parentheses: M, male; F, female; U, sex unknown.

^aSubsamples of Howells (1973, 1989) populations.

The two samples represent distinct populations separated not only in space but probably also in time. They were included in the same group here as they are closer to each other than to any other population studied (Ferembach, 1962). Due to the poor preservation of this material, the Epipaleolithic sample that was complete enough to be included in the analysis was substantially smaller than that of the other recent human populations (see Table 1). A mixed Eurasian population, represented by samples of six individuals each from four localities across Western Eurasia, was also measured, so as to better represent a sample that would simulate the variation in the fossil sample drawn from multiple populations from the same general geographical area.

Only adult crania were included, as determined by a fully erupted permanent dentition. Sex was unknown in most cases and was assessed by inspection during study and following Howells' sexing assessments. Where possible, equal numbers of males and females were measured. However, as sex is unknown for the fossil specimens, the two sexes were pooled in the analysis.

The chimpanzee comparative sample consisted of 94 individuals, representing the two species *Pan paniscus* and *P. troglodytes*, as well as two subspecies of the common chimpanzee, *P. t. schweinfurthii* and *P. t. troglodytes* (Table 1). Only adult and wild-shot specimens were included, as determined by fully erupted permanent dentition and museum tags and catalog information. As all available specimens were measured, the chimpanzee samples do not include equal numbers of males and females. As with the modern human specimens, the chimpanzee male and female samples were pooled.

The fossil human sample included Neanderthal specimens from Europe and the Near East; Late Pleistocene early anatomically modern humans from the Near East; and Late Paleolithic anatomically modern humans from Europe (Table 2). In cases where the original fossils were unavailable due to limited access to, or loss of, the originals, high quality casts from the Anthropology Department of the American Museum of Natural History were measured.

3.2. Data

3.2. Data

The data were collected in the form of three-dimensional coordinates of craniofacial landmarks using a Microscribe 3DX portable digitizer (Table 3; Fig. 1). Only midline and right side landmarks were used in the analysis. Landmarks are defined

Table 2
List of fossil human specimens measured

Neanderthal	Late Paleolithic	Early anat. modern
Circeo 1 (Step 1, 2)	Cro Magnon 1 (Step 1, 2, *)	Skhul 5 (Step 1, 2, *)
Amud 1 (Step 1, 2)	Predmosti 3 (Step 1, 2, *)	Qafzeh 9 (Step 2)
La Ferrassie 1 (Step 1, 2, *)	Mladec 1 (Step 1, 2)	
La Chapelle (Step 1, 2, *)	Cro Magnon 2 (Step 2, *)	
Shanidar 1 (Step 1, 2, *)	Predmosti 4 (Step 2, *)	
Tabun C1 (Step 2)	Mladec 5 (Step 2, *)	
Spy 2 (Step 2)		
La Quina 5 (Step 2, *)		

In parenthesis are indicated the levels of analysis in which each specimen was used. Asterisks indicate specimens for which casts were used.

Table 3
List of landmarks collected, levels of analysis in which each landmark was included and measurement error for each landmark

Landmarks	Intra-observer error		
	Step	Deviation	% Error
1. Inion	(1, 2)	0.16	0.20
2. Asterion	(1, 2)	0.34	1.03
3. Lambda	(1, 2)	0.06	0.06
4. Bregma	(1, 2)	0.10	0.09
5. Glabella	(1, 2)	0.08	0.37
6. Nasion	(1)	0.06	0.29
7. Prosthion	(1)	0.31	0.41
8. Porion	(1, 2)	0.31	1.43
9. Auriculare	(1, 2)	0.24	0.95
10. Parietal notch	(1, 2)	0.15	0.56
11. Mastoidiale	(1, 2)	0.08	0.24
12. Medial end of the petro-tympanic crest at the level of the carotid canal	(1, 2)	0.27	0.92
13. Deepest point of the lateral margin of the articular eminence	(1)	0.24	0.66
14. Most inferior point on the entoglenoid pyramid	(1)	0.21	0.70
15. Lateral end of the superior nuchal line (the most lateral extent of the splenius capitis scar on the occipital bone)	(1, 2)	0.39	1.04
16. Superior aspect of the zygomatico-temporal suture	(1)	0.11	0.16
17. Inferior aspect of the zygomatico-temporal suture	(1)	0.16	0.30

Deviations are reported in millimeters.

in geometric morphometrics as homologous points that can be reliably and repeatedly located in all specimens under study. There are several kinds of landmarks as defined by Bookstein (1990) and Valeri et al. (1998). Most landmarks used here are of either type I or II, with the exception of porion and auriculare, which can be considered type III landmarks. No ‘fuzzy’ landmarks were used. Landmarks were digitized from the basicranium, the vault and the face, in an effort to represent

cranial morphology as fully as possible. Most are standard osteological landmarks, following the definitions of Howells (1973), except for four (landmarks 12–15, Table 3). Measurement error was calculated for each landmark based on 10 replicates of the same specimen. Error was assessed for each landmark by calculating the deviation around the mean distance of that landmark from the centroid (mean of all coordinates). This deviation was then expressed as a percentage

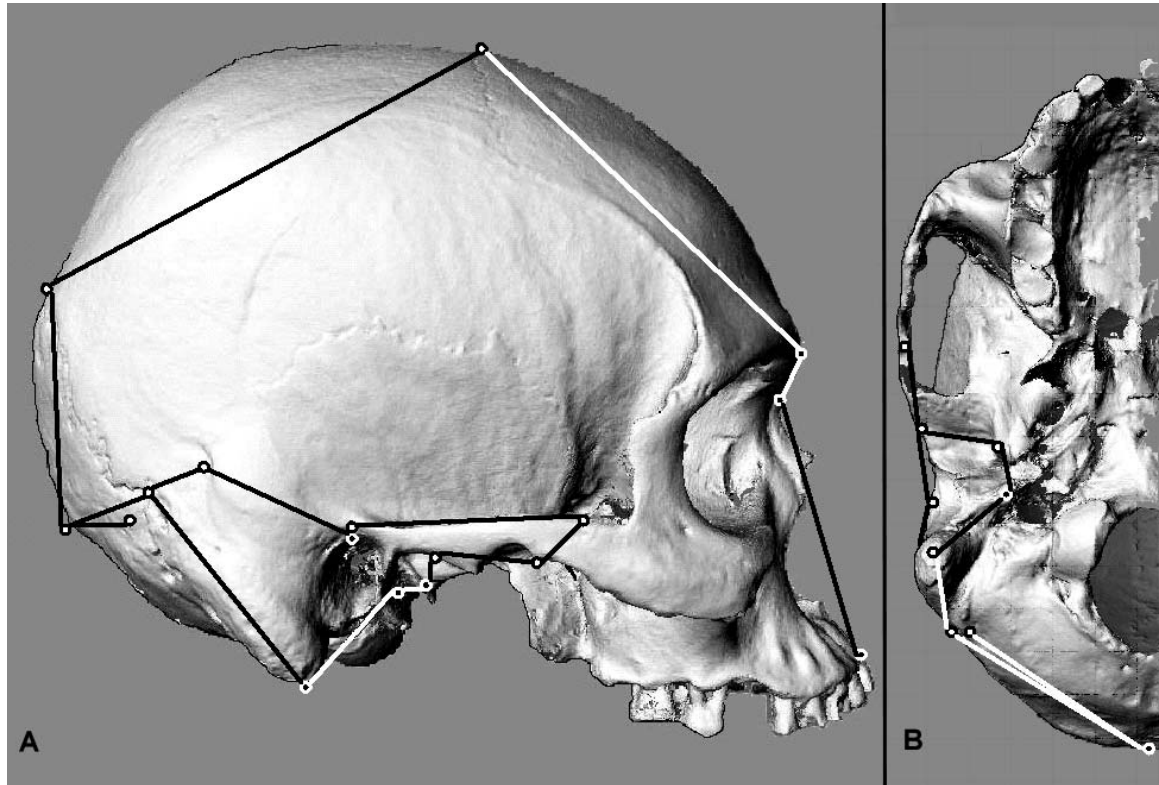


Fig. 1. Landmarks used in this analysis. Landmark definitions are given in Table 3. The lines connecting the landmarks do not represent data. They are links used for purposes of visualization.

of the mean distance from the centroid. Measurement error ranged from 0.06 to 0.39 mm, and from 0.06 to 1.43% and was similar across all landmarks (Table 3). This level of error is minimal and is within the range reported for similar methods (see Singleton, 2002).

The craniofacial morphology represented by the landmarks collected is thought to differentiate Neanderthals from modern humans in such traits as the height of the vault, the degree of midfacial projection, the height of the occipital plane and the relative size of the mastoid process (Boule, 1911–1913; Boule and Vallois, 1957; Santa Luca, 1978; Stringer and Trinkaus, 1981; Trinkaus and Smith, 1985; Vandermeersch, 1985; Hublin, 1988). It is also thought to differentiate the two chimpanzee species, as bonobos are found to differ from common chimpanzees in the development of the splanchnocranium relative to the neurocranium and

in the width of the cranium relative to its length (Shea, 1984).

3.3. Data reconstruction and levels of analysis

Because morphometrics does not accommodate missing data, it was found necessary to allow some data reconstruction and to introduce levels of analysis in which subsets of landmarks were considered. Minimal reconstruction by estimation was allowed during data collection for specimens where very little damage was observed in a particular area of interest. This was done through estimation of the position of the structure of interest using the morphology of the preserved surrounding areas and was only allowed in specimens showing minimal damage. Although only right side landmarks were used in this analysis, left side landmarks were

Table 4
Estimated error resulting from reconstructing missing bilateral landmarks by reflection

Landmarks	Reflection error	
	Mean distance	Standard deviation
1	0.0098	0.0086
2	0.0225	0.0116
3	0.0121	0.0010
4	0.0164	0.0156
5	0.0202	0.0192
6	0.0197	0.0181
7	0.0256	0.0192
8	0.0197	0.0101
9	0.0207	0.0100
10	0.0265	0.0152
11	0.0222	0.0115
12	0.0230	0.0122
13	0.0217	0.01063
14	0.0217	0.01192
15	0.0236	0.01215
16	0.0224	0.01224
17	0.0231	0.01295

Deviations are reported in millimeters.

used for reconstruction of missing right side landmarks by mirror imaging, as the majority of fossil specimens still exhibited many missing landmarks. Specimens with missing data were least-squares superimposed with their reflections using GRF-ND. This has the effect of canceling out midline asymmetry. The coordinates for each of the missing landmarks were then substituted from the fitted homologous landmark in the reflection. In order to assess the mean error associated with this procedure, a reflection of the entire dataset was constructed by inverting the sign of one of the dimensions. This reflected dataset was appended to the original dataset and both reflected and non-reflected specimens were Procrustes registered, again having the effect of canceling out the midline asymmetry. All right side landmarks and their reconstructed, mirror imaged left side homologues were then compared. For each landmark the mean Euclidean distance between the true landmark and its reconstructed position, as well as the standard deviation around it, was calculated (Table 4). The mean error across landmarks associated with the reflection procedure was quite small, ranging from 0.0098 to 0.0265 mm.

In order to maximize the number of fossil specimens included, the analysis was conducted in two steps, each varying in the number of landmarks used and the number of fossil and recent specimens complete enough to be included (Tables 1–3). Step 1 included 17 landmarks, five Neanderthal specimens and three Late Paleolithic specimens, while Step 2 included 11 landmarks, eight Neanderthal and six Late Paleolithic specimens.

3.4. Geometric morphometrics

The coordinates were processed using generalized procrustes analysis (GPA), which superimposes the landmark coordinates configurations of the specimens and scales them for size, so that the differences they exhibit are due to ‘shape’ (Rohlf, 1990; Rohlf and Marcus, 1993; Slice, 1996). The Procrustes methods have been shown to have very high statistical power among alternative geometric morphometric approaches (Rohlf, 2000). The specimen configurations were translated to common origin, scaled to unit centroid size (the square root of the sum of squared distances of all landmarks to the centroid of the object, the measure of size used here) and rotated according to a least-squares criterion. Superimposition was performed using the software GRF-ND and Morpheus (Slice, 1992, 1994–1999).

The fitted coordinate configurations resulting from these procedures are thought to lie in Kendall’s shape space (Rohlf, 1996). Recently, Slice (2001) found that instead they lie in a hemispherical variant of this shape space. As in both cases shape space is non-Euclidean, a projection of these coordinates to tangent space is usually recommended for statistical analysis. However, biological data are restricted in their variation and the shape space coordinates are almost identical to their projections in tangent space (Slice, 2001). This assumption was tested using TPSSMALL (Rohlf, 1998), which compares the Procrustes distances to the Euclidean distances. The correlation between the two distances was found to be very strong (correlation 0.99999 and root MS error 0.00007). The statistical analysis was therefore performed on the fitted coordinates themselves.

Geometric morphometrics methods present several advantages over traditional morphometrics. In this kind of analysis the geometry of the object studied is better preserved in the data, the original form can be recovered better from the coordinates of the landmarks recorded and far less information is lost about the original material studied. These techniques allow one to identify the landmarks where shape variation occurs, as well as the relative levels of variation at each landmark (Rohlf and Marcus, 1993; Yarooh, 1996; O'Higgins, 2000). Geometric morphometrics also provide a way of quantifying shape differences, and therefore differences in character states, of variable traits which are difficult to measure with traditional caliper measurements (Dean, 1993). Finally, geometric methods can readily provide illustrations of the shape changes between specimens in specimen space (Rohlf and Marcus, 1993; Lynch et al., 1996). Here the mean configurations of the groups used are compared to each other (Fig. 2). Geometric morphometric methods have recently been applied to primatology (O'Higgins and Jones, 1998; Collard and O'Higgins, 2000; Singleton, 2002; Frost et al., in prep.), human variation (Ahlström, 1996; Wood and Lynch, 1996; Hennessy and Stringer, 2002; Rosas and Bastir, 2002) and paleoanthropology (Dean, 1993; Yarooh, 1996; Penin, 1997; Dean et al., 1998; Bookstein et al., 1999; Delson et al., 2001; Ponce de León and Zollikofer, 2001).

3.5. Statistical methods

The fitted coordinate configurations of the specimens were analyzed using principal components analysis (PCA), in order to explore how variation is partitioned within and among the samples, as well as to achieve data reduction. An ANOVA was performed on the PCA scores to determine the significance of population effects along each component. A Bonferroni *t*-test (alpha set to 0.05) was performed on all pairwise comparisons of the population means of the principal component (PC) scores, in order to detect significant differences between groups. This test is conservative, therefore significant differences found at

the preset alpha level have a somewhat greater level of significance. The influence of each landmark on each PC was assessed by inspection of the eigenvectors of each variable for that component and by visual inspection of the shape differences along each eigenvector in GRF-ND (Slice, 1996). Canonical variates analysis (CVA) was then conducted on the PC scores, in order to maximize the separation between groups. Unlike the PCA, this analysis uses group membership information. The group information used here was population membership rather than species or genus information, so as not to bias the results toward separation of pre-designated species. The CVA was performed on the PC scores rather than on the coordinates, so as to reduce the number of variables analyzed. The first 40 PCs were used for the first step of analysis, accounting for more than 99.9% of the total variance. All the non-zero PCs (26) were used in the second step of analysis.

Mahalanobis D^2 matrices were obtained for the groups included in the analysis correcting for unequal sample sizes (Marcus, 1993), reported in Appendix A. The analysis was first performed on the combined human and chimpanzee samples. It was then repeated on the chimpanzee and the human samples separately, in order to test the consistency of the chimpanzee model, as the distances among the chimpanzee taxa may be underestimated in the combined sample analysis due to the greater variation in the human sample. The combined sample Mahalanobis distances were used to produce cluster diagrams. When performing a Mahalanobis distance analysis, the position of singletons and groups comprising very few specimens relative to other groups can be misleading, due to misrepresentation of the variation in their groups. False singleton situations, produced by randomly taking specimens out of the modern human sample and treating them as unknowns, showed that these specimens exhibited a very large D^2 value to their own population in some, but not all, cases. Therefore, the Mahalanobis distances between singletons, or two-specimen groups, and other groups may be overestimated and were excluded from the cluster analyses. These distances are reported in the distance matrices for the sake of completeness.

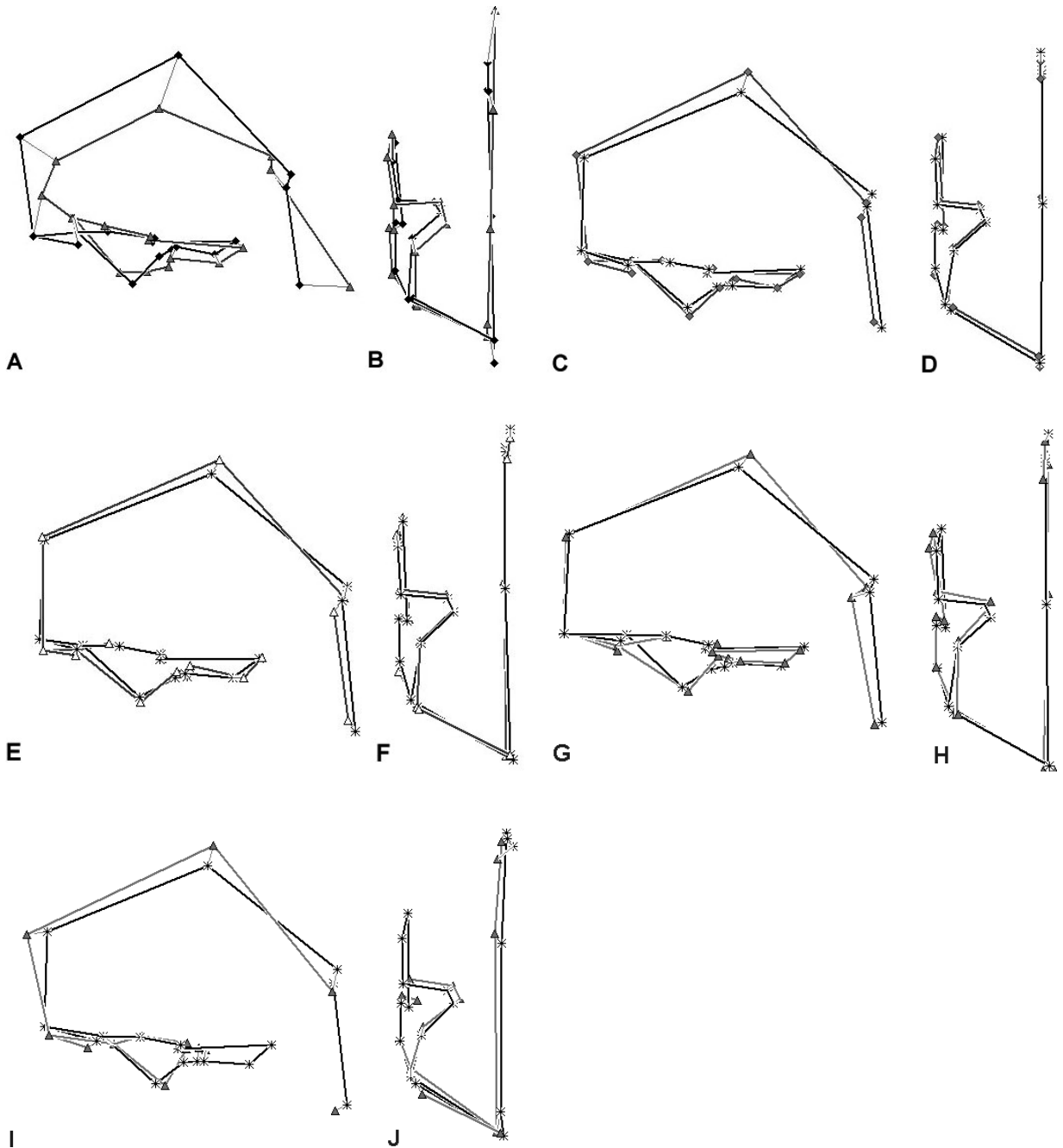


Fig. 2. Superimposed mean configurations for the groups used in the analysis. The specimens are scaled for size. (A,B) Mean modern human and chimpanzee configurations, lateral and ventral views. (C,D) Mean modern human and Neanderthal configurations, lateral and ventral views. (E,F) Mean Late Paleolithic and Neanderthal configurations. (G,H) Skhul 5 and mean Neanderthal configurations. (I,J) Qafzeh 9 and Neanderthal mean configurations. Note that nasion, as well as the two landmarks on the zygomatico-temporal suture are missing in Qafzeh 9, which was only included in Step 2. Modern humans, solid diamonds; Chimpanzees, grey up triangles; Neanderthals, stars; Late Paleolithic specimens, open up triangles; Skhul 5, Qafzeh 9, grey up triangles.

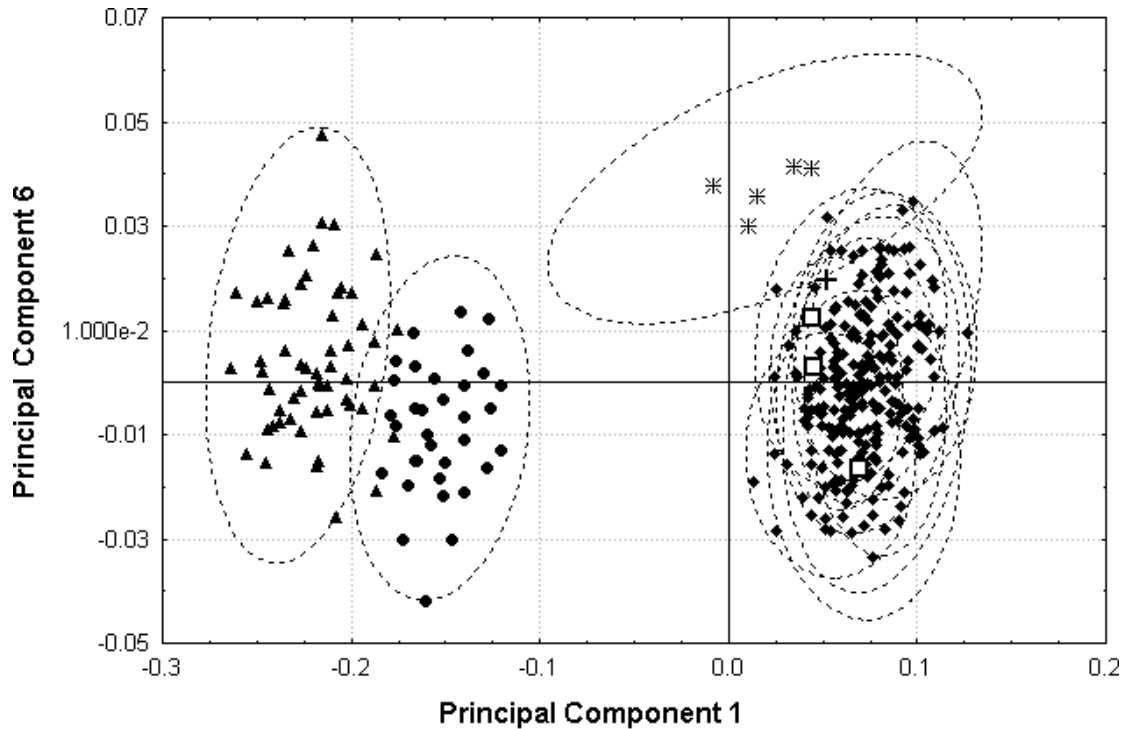


Fig. 3. PCA, Step 1. PCs 1 and 6 are shown. Diamonds, modern humans; stars, Neanderthals; open squares, Late Paleolithic Europeans; cross, Skhul 5; up triangles, *P. troglodytes*; circles, *P. paniscus*. The dotted lines represent 95% confidence ellipses by population.

4. Results

4.1. Step 1

PC 1 (78.8% of the total variance, Fig. 3) separated humans from chimpanzees, the two chimpanzee species from each other and Neanderthals from modern humans. Neanderthals were found to be significantly different from all modern human populations (α set to 0.05), including the Late Paleolithic specimens, in their PC 1 scores, although there was some overlap between the extreme of the modern human range and the two Near Eastern Neanderthals included in Step 1, Shanidar 1 and Amud 1. *P. paniscus* were also significantly different from both *P. troglodytes* populations, while all chimpanzees were significantly different from all humans. Neanderthals were also found to be significantly different from

all modern human groups in their PC scores on PC 6 (1.2% of the total variance, Fig. 3). PC 2 (2.7% of the total variance) separated the two chimpanzee species, *P. paniscus* being significantly different from both *P. troglodytes* populations. The Late Paleolithic European specimens were not separated from recent humans along the PCs that separated Neanderthals from modern humans.

The separation of the groups along PC 1 was driven above all by the position of bregma and prosthion. Bregma was found to be much higher in modern humans relative to both chimpanzees and Neanderthals. It was also higher in *P. paniscus* relative to *P. troglodytes*. Prosthion was much more anteriorly projecting relative to the rest of the cranium in chimpanzees as compared to humans. A more anterior placement of prosthion also characterized *P. troglodytes* relative to *P. paniscus* and Neanderthals relative to modern

humans. Inion and lambda also influenced PC 1. Inion was placed much more superiorly and anteriorly in chimpanzees relative to humans, reflecting their short occipital plane and long nuchal plane. It was also placed more antero-superiorly in *P. troglodytes* relative to *P. paniscus*, and more posteriorly and superiorly in Neanderthals relative to modern humans, reflecting both a shorter and a more posteriorly projecting occipital plane. Lambda was also placed much more inferiorly and anteriorly in chimpanzees relative to humans. It was positioned more anteriorly in Neanderthals relative to modern humans, perhaps suggesting a lambdoid depression, often associated with an occipital bun. Finally, PC 1 was also influenced by the position of glabella and nasion. These landmarks were much more superiorly and posteriorly positioned in chimpanzees relative to humans, being almost at the level of bregma and reflecting a low neurocranium compared to the high and rounded vault in humans, and a much longer and anteriorly projecting face. Glabella and nasion were even more superiorly placed in *P. troglodytes* relative to *P. paniscus*, and more anteriorly and slightly more superiorly placed in Neanderthals relative to modern humans (Fig. 4a, b). PC 6, which also separated Neanderthals from modern humans, was influenced mostly by the position of asterion and the lateral end of the superior nuchal line, which were placed more laterally in Neanderthals relative to modern humans, as well as by the position of bregma, which was much lower in Neanderthals (Fig. 4c, d). The more lateral position of asterion and the lateral end of the superior nuchal line in Neanderthals may reflect their relatively wide occipital bone (Heim, 1974), while the lower position of bregma indicates a lower vault in this group.

The CVA was conducted on the first 40 PCs, accounting for 99.9% of the total variance. The first canonical axis (84.9% of the total variance, Fig. 5) separated humans from chimpanzees, as well as Neanderthals from modern humans and *P. paniscus* from *P. troglodytes*. This canonical axis was most heavily influenced by PC 1. The second canonical axis (3.5% of the total variance) separated the two chimpanzee species. This axis was most heavily influenced by PC 2.

The unbiased Mahalanobis D^2 was calculated (reported in Appendix A). The distance between Neanderthals and all modern human populations, including the Late Paleolithic group, was always found to be greater than the distances between any two modern human groups. It was always greater than, or equivalent to, the distances found between the two chimpanzee species. The distance between Neanderthals and the Late Paleolithic Europeans was the smallest distance between Neanderthals and any modern human group, but it was still equivalent to the other Neanderthal–modern human distances as well as to the distances between the two chimpanzee species. The distances between the Late Paleolithic specimens and the recent human groups were comparable to those found among recent human populations. This group was found to be closest to the Australian and Melanesian Tolai populations. Skhul 5 showed very large distances from both Neanderthals and modern humans, but these distances may be over-estimated due to the sample size of 1 for the early anatomically modern group.

The Mahalanobis D^2 matrices were also calculated for the human and chimpanzee samples separately and the distances compared. As shown by a Mantel test for correlation between matrices (Pearson correlation, one-tailed test, 999 permutations), the distance matrices from the combined sample and separate sample analyses for both taxa were very strongly correlated ($p \leq 0.0001$), indicating very similar results for the two analyses. Neanderthals were now found to be separated from modern human populations, including the Late Paleolithic specimens, by even greater distances than found in the combined sample analysis. These were always by much greater than those between the two chimpanzee species.

The combined sample Mahalanobis distances were used to generate a cluster diagram (Fig. 9a). Chimpanzees clustered on a different branch from all humans, while Neanderthals were very widely separated from recent human populations. The Late Paleolithic specimens were placed very close to the recent human population cluster. Some geographic clustering is present among recent human groups, with the two European

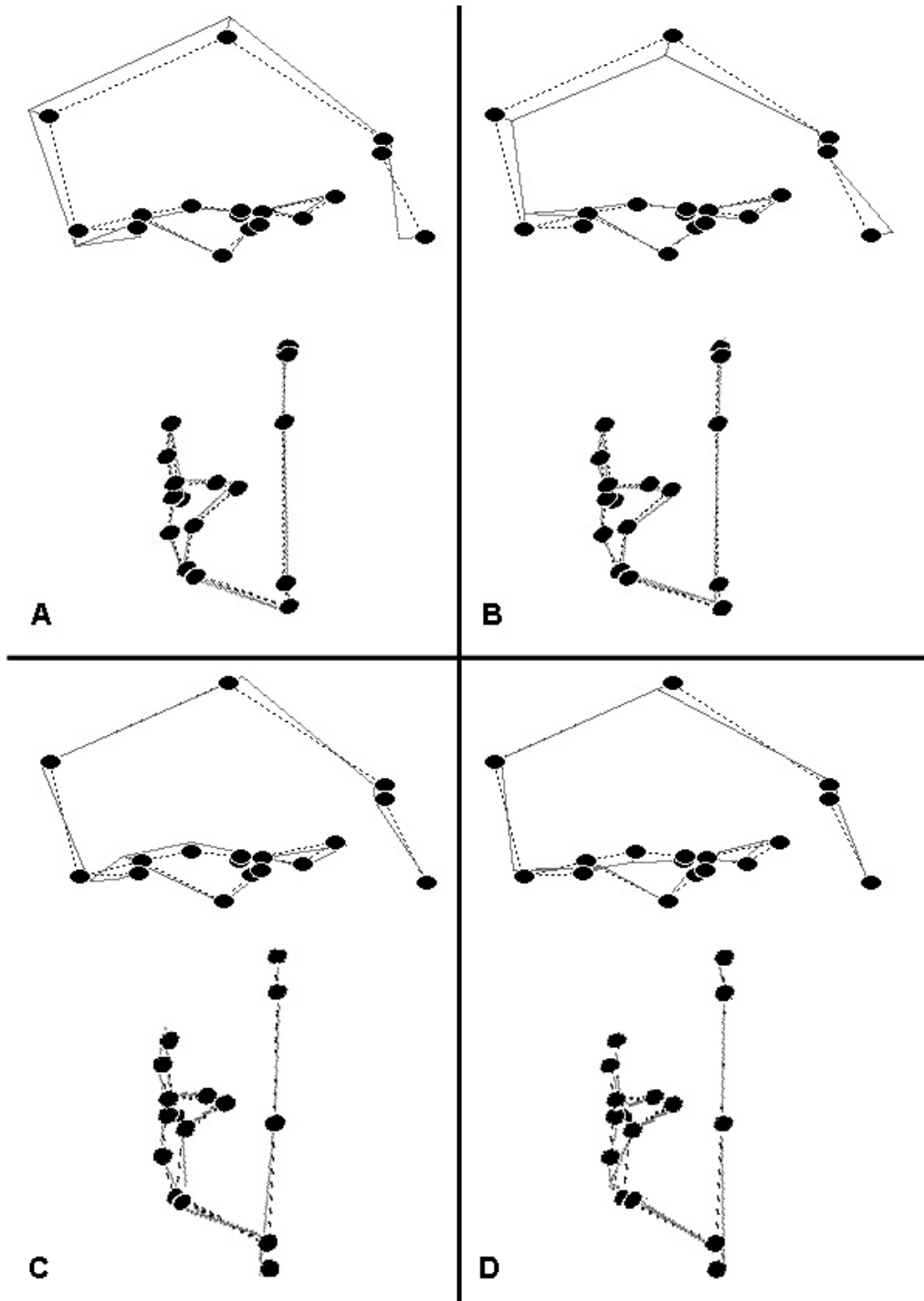


Fig. 4. Shape differences along PC 1 (a, b) and 6 (c, d), Step 1. The dotted line represents the consensus configuration. (A) Modern human end of PC 1, lateral (top) and ventral views. (B) Chimpanzee end of PC 1, lateral and ventral views. (C) Modern human end of PC 6, lateral and ventral views. (D) Neanderthal end of PC 6, lateral and ventral views.

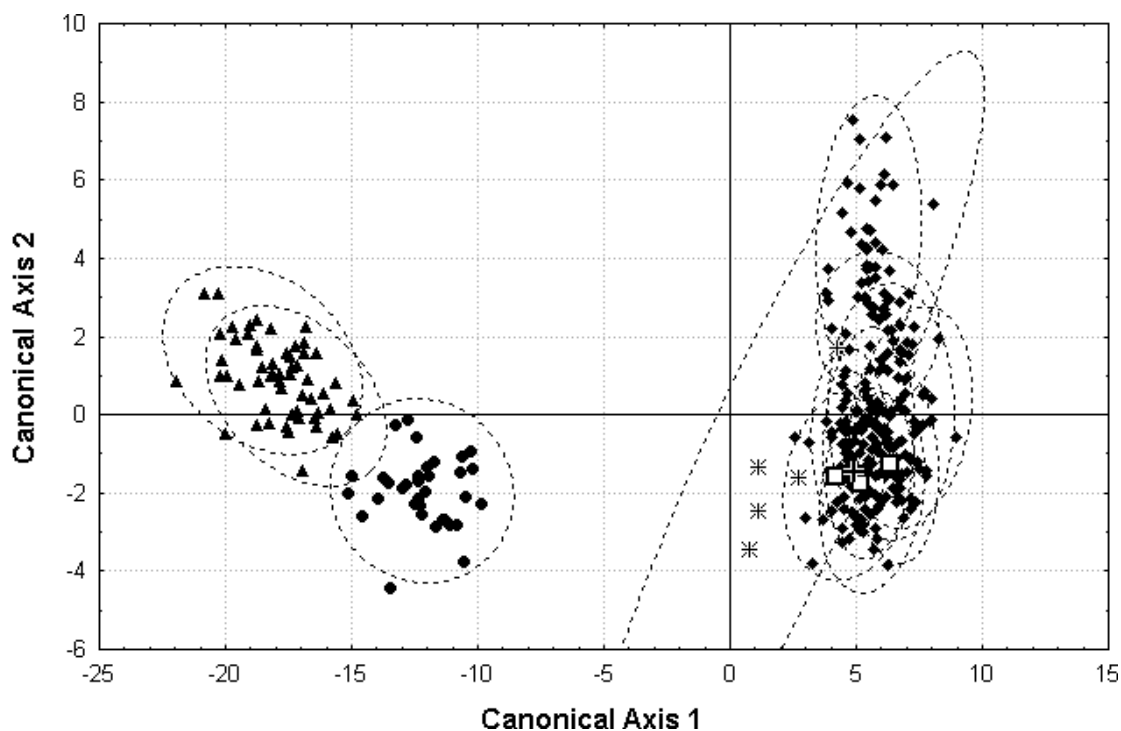


Fig. 5. Canonical variates analysis, Step 1. Canonical axes 1 and 2 are shown. Labels as in Fig. 3. The dotted lines represent 95% confidence ellipses by population.

populations and the Australian–Melanesian pair grouping closely together.

4.2. Step 2

Results were very similar to those reported for Step 1. Neanderthals were separated from modern humans along PC 1 (accounting for 74.9% of the total variance, Fig. 6). This component also separated all humans from chimpanzees, *P. paniscus* from *P. troglodytes* and the two subspecies of *P. troglodytes*. Neanderthals were significantly different from all modern human populations, including the Late Paleolithic specimens, in their PC 1 scores. As in Step 1, Shanidar 1 and Amud 1, however, overlapped with the modern human range along this component. Furthermore, *P. paniscus* were significantly differently from both *P. troglodytes* populations along PC 1, as were all human groups from all chimpanzee groups. PC 2

(4.1% of the total variance, Fig. 6) also separated the two chimpanzee species, *P. paniscus* again being significantly different from both *P. troglodytes* groups in their PC 2 scores. The shape differences along PC 1 were very similar to those reported for PC 1 in Step 1, and include differences in the position of inion, lambda, bregma and glabella (Fig. 7). The Late Paleolithic Europeans were not separated from recent humans.

The CVA was conducted on all the PCs (26), accounting for 100% of the total variance. Neanderthals were separated from modern humans along canonical axis 1 (accounting for 82.5% of the total variance, Fig. 8). This axis also separated humans from chimpanzees and was most heavily influenced by PC 1. *P. paniscus* and *P. troglodytes* were separated along the third canonical axis (3.3% of the total variance, most heavily influenced by PCs 2 and 5).

The unbiased Mahalanobis D^2 matrix was calculated, yielding results very similar to those of

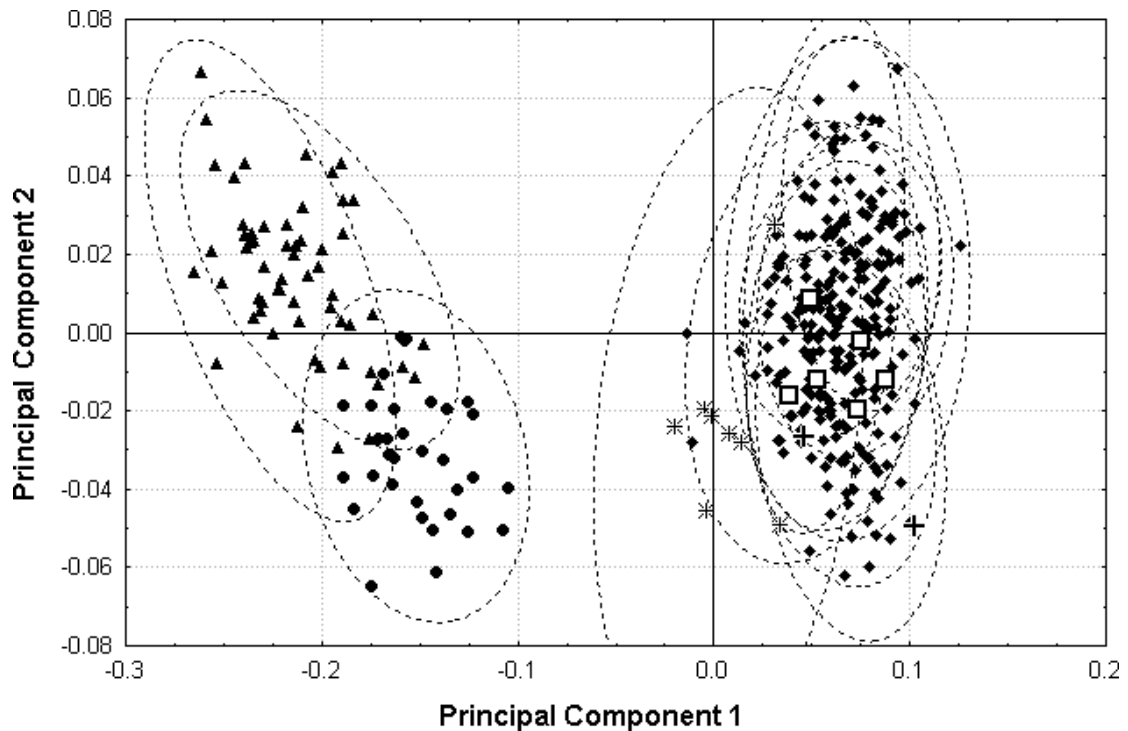


Fig. 6. PCA, Step 2. Labels as in Fig. 3. The two modern human outliers are from the Inugsuk Eskimo population. The dotted lines represent 95% confidence ellipses by population.

Step 1. Neanderthals showed distances from all modern human groups that were greater than or equivalent to those found between the two chimpanzee species. However, here the greatest distance between two recent human populations, that between the Andamanese and the Khoisan, was greater than the smallest distances between Neanderthals and recent humans. Neanderthals were closest to the Inugsuk Eskimo population, and their distance to the Late Paleolithic Europeans was equivalent to the other Neanderthal–modern human distances. The distances between the Late Paleolithic specimens and the recent human groups were again comparable to those found among recent human populations. These specimens were found to be closest to the Austrian Berg population. Finally, two early anatomically modern human specimens were included in this step of analysis, Skhul 5 and Qafzeh 9. These were found to be again very distant from all recent human populations and from Neanderthals, but relatively

close to the Late Paleolithic group. As in Step 1, these large distances may be overestimated due to the very small sample size. The unbiased Mahalanobis D^2 matrices for the separated human and chimpanzee samples were very similar to those obtained in the combined sample analysis ($p \leq 0.005$). The cluster diagram generated from the combined sample Mahalanobis D matrix is shown in Fig. 9b. Here the Late Paleolithic group is placed within the recent human cluster and clustering with the Epipaleolithic population.

5. Discussion

Both steps of analysis yielded similar results. The morphological distances between Neanderthals and all modern human populations, including the Late Paleolithic specimens, were found to be greater than the distances among modern human groups. The one exception found is

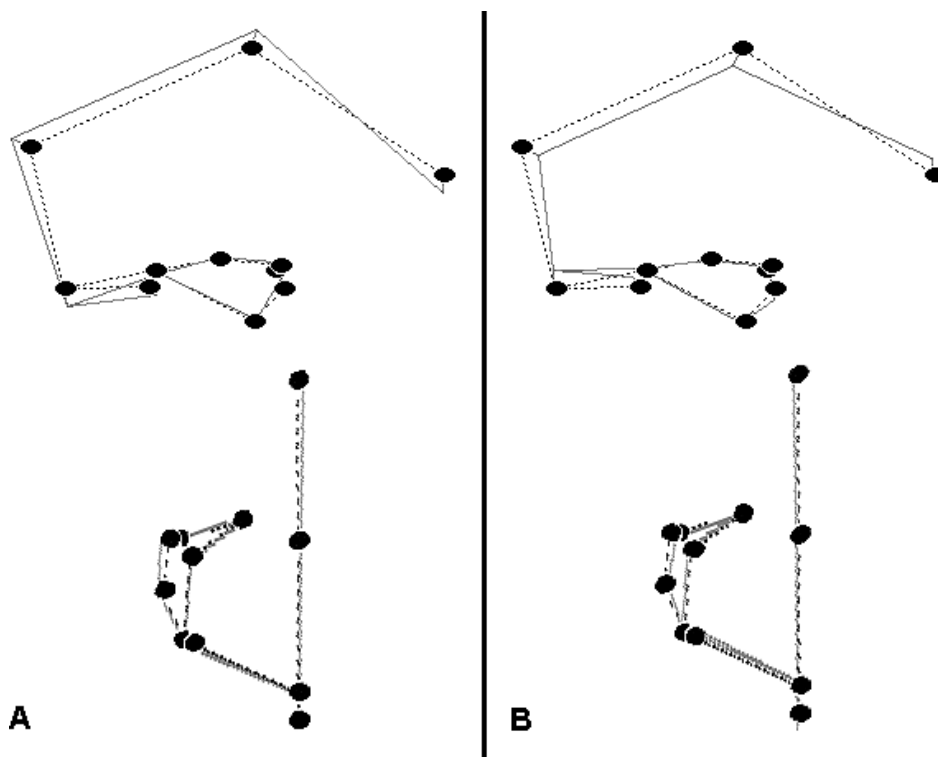


Fig. 7. Shape differences along PC 1, Step 2. The dotted line represents the consensus configuration. (A) Modern human end of PC 1, lateral (top) and ventral views. (B) Chimpanzee end of PC 1, lateral and ventral views.

the Andamanese–Khoisan pairwise comparison in Step 2, which showed a distance between these groups that is equivalent to the smallest Neanderthal–modern human distance. The Neanderthal–modern human distances are also greater than or equivalent to the distances between the two chimpanzee species. The morphological distances among modern human populations are always lower than those between the two chimpanzee species in Step 1. This is not always the case in Step 2. This finding may result from the removal of half of the facial landmarks used and may reflect the importance of these landmarks in differentiating *P. paniscus* from *P. troglodytes*.

The general dichotomy between Neanderthals and modern humans is in agreement with previous multivariate analysis of craniofacial measurements (Stringer, 1974, 1989; Bräuer and Rimbach, 1990; Bräuer, 1992; Stringer, 1992; Turbón et al., 1997). This is the first study to compare general cranio-

facial morphological distances between Neanderthals and modern humans and Neanderthals and Late Paleolithic Europeans to those observed between the two chimpanzee species. The finding of greater morphological distances between Neanderthals and modern humans and Neanderthals and Late Paleolithic Europeans than between *P. paniscus* and *P. troglodytes* is in agreement with previous comparisons of particular cranial regions (Harvati, 2001a,b, 2002). It also agrees with the findings of Schillaci and Froelich (2001), who compared the genetic distance and differentiation between Neanderthals and Late Paleolithic Europeans to those between macaque species based on morphological traits. These results are consistent with the predictions of Hypothesis A, that Neanderthals represent a different species from modern humans. However, this support is not unequivocal. The large Andamanese–Khoisan morphological distance, as well as the somewhat small distances

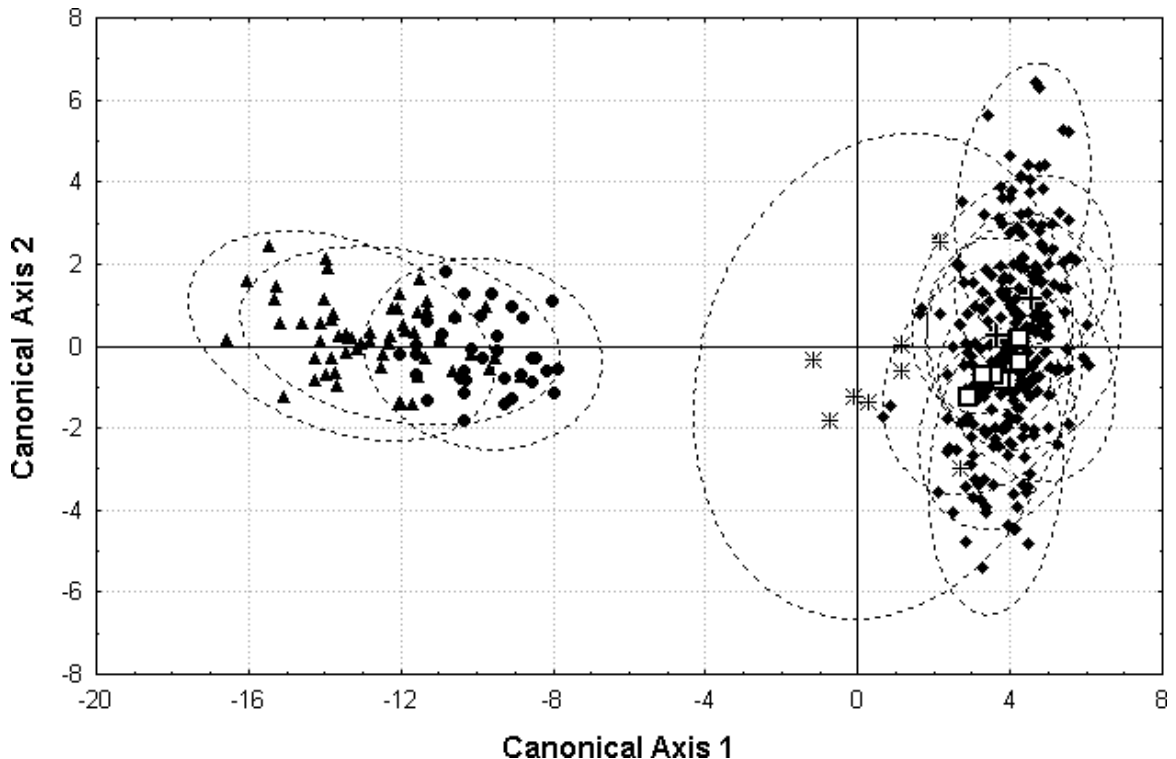


Fig. 8. CVA, Step 2. Labels as in Fig. 3. The dotted lines represent 95% confidence ellipses by population.

between the two chimpanzee samples relative to those among modern human groups, suggest that intra- and inter-specific morphological differentiation in humans may follow a different pattern from that observed in *Pan*. The development of additional models to be applied to the Neanderthal–modern human comparison would help resolve this issue.

The Neanderthal mean configuration shows several differences from that of all recent humans (Fig. 2c, d). These include: a much lower vault, reflected by a more inferior position of bregma and a superior placement of glabella; a shorter and wider occipital plane, as seen in the superior placement of inion and of the lateral end of the superior nuchal line; a longer and more anteriorly projecting face, reflected in the more superior and anterior position of glabella and nasion and the more inferior and anterior placement of prosthion; a smaller mastoid process, seen in the superior position of mastoidale; a more inferior and lateral

position of the root of the articular eminence at the margin of the glenoid fossa, suggesting a shallower and wider glenoid fossa; and a somewhat anterior placement of lambda, again suggesting a lambdoid depression, often associated with occipital buns. These differences are consistent with previous descriptions (Boule, 1911–1913; Boule and Vallois, 1957; Vallois, 1969; Heim, 1974; Santa Luca, 1978; Stringer and Trinkaus, 1981; Trinkaus and Smith, 1985; Vandermeersch, 1985; Hublin, 1988). A subset of these shape differences were found to separate Neanderthals from modern humans in the statistical analysis, including a lower vault, a longer and more anteriorly projecting face, a shorter occipital plane and a more anterior placement of lambda, perhaps reflecting lambdoid flattening associated with occipital bunning. A wider occipital bone was also found to separate Neanderthals from modern humans in Step 1 but not in Step 2. Contrary to the findings of Yarooh (1996), who did not find the Neanderthal cranial

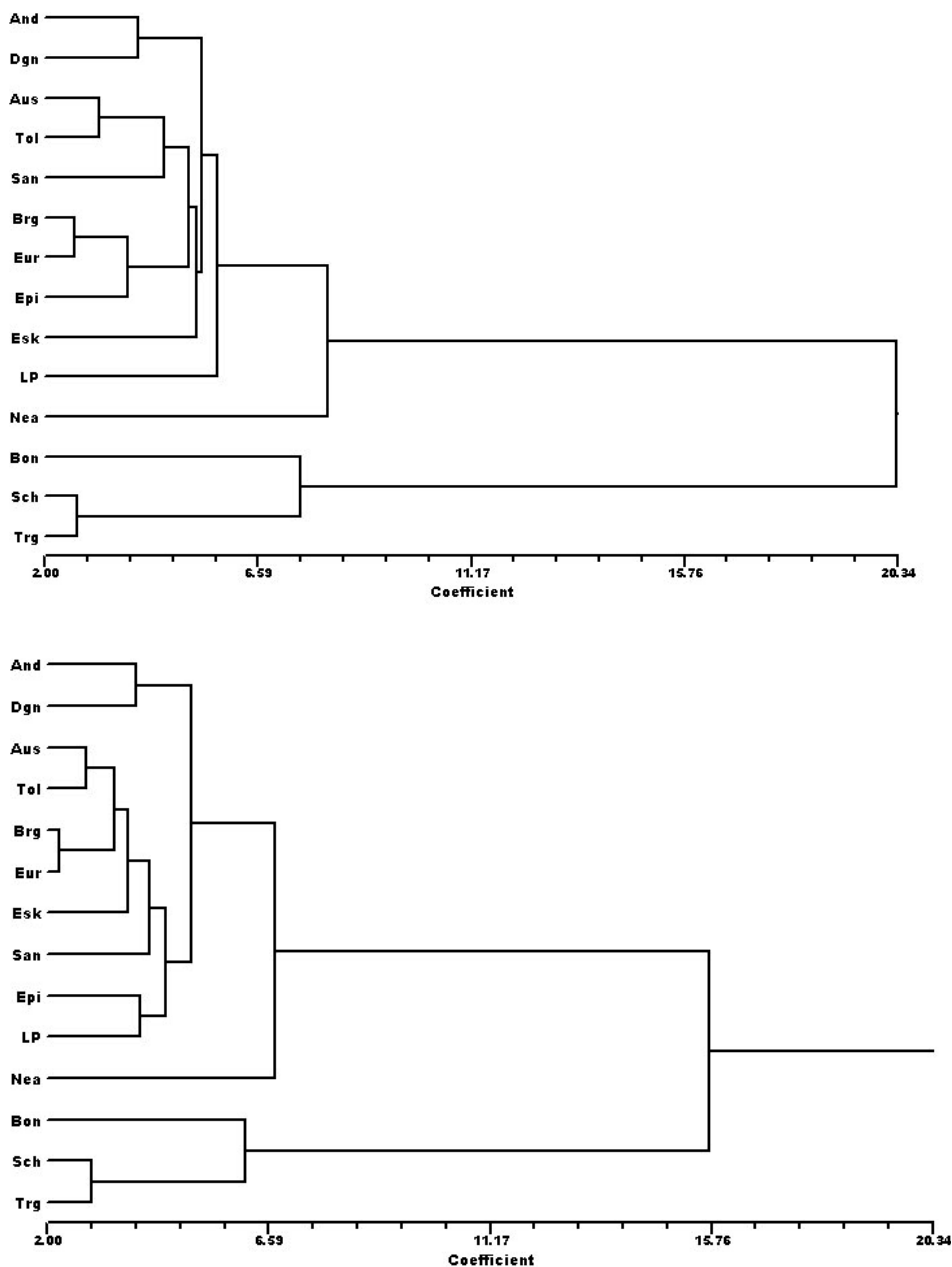


Fig. 9. Cluster diagrams using the unweighted pair group method with arithmetic mean (UPGMA), based on the Mahalanobis distances between groups obtained from the canonical variates analysis. AND: Andamanese, AUS: Australian, BRG: Berg, DGN: Dogon, EPI: Epipaleolithic, ESK: Inugsuk Eskimo, EUR: mixed W. Eurasian, SAN: Khoisan, TOL: Tolai, LP: Late Paleolithic, NEA: Neanderthal, BON: *P. paniscus*, SCH: *P. t. schweinfurthii*, TRG: *P. t. troglodytes*. A: Step 1, B: Step 2.

shape to be unique based on thin plate spline analysis of two-dimensional landmarks, the present study did find craniofacial morphology to

differentiate Neanderthals and modern humans, although there was limited overlap between the extremes of the ranges of the two groups.

The Neanderthal sample was not subdivided into Eastern and Western Neanderthals due to its small sample size. The first step of the analysis included two Eastern Neanderthal specimens, Amud 1 and Shanidar 1, while Tabun C1 was added in the second step. In both steps of the analysis Amud 1 and Shanidar 1 overlapped with modern humans along PC 1, which separated Neanderthals from modern humans, although Tabun C1 did not. PC 1 was influenced by the position of bregma, which was much lower in Neanderthals relative to modern humans, reflecting a lower vault. Both Amud 1 and Shanidar 1 show a somewhat higher position of bregma relative to the mean Neanderthal configuration, reflecting a relatively higher vault. A higher vault has been noted previously for the Eastern Neanderthal specimens (Stringer and Trinkaus, 1981; Trinkaus, 1983; Stringer et al., 1984; Condemi, 1992), and is consistent with previous observations of geographic variability within the Neanderthal sample, as the Eastern Neanderthals are often considered to exhibit less pronounced Neanderthal features than the 'classic' European Neanderthals (Stringer and Trinkaus, 1981; Vandermeersch, 1989).

Neanderthals were found to be closest in Mahalanobis D^2 to the Late Paleolithic European group among modern human populations in the first step of the analysis, a finding that is at first consideration consistent with one of the predictions of Hypothesis B, that Neanderthals contributed to the evolution of modern humans in Europe. However, this distance is still very large and it is equivalent to the distances between Neanderthals and other modern human populations, as well as to that between the two chimpanzee species. In Step 2, where additional Late Paleolithic specimens were included, Neanderthals were found to be closest to the Inugsuk Eskimo, this distance also being equivalent to the distances between the two chimpanzee species. The Neanderthal mean configuration differed from the Late Paleolithic European mean configuration in the same features that it differed from the mean configuration of all recent humans (Fig. 2e, f). Compared to the recent human mean configuration, the Late Paleolithic mean configuration resembled the Neanderthal one only in having a slightly lower

vault, reflected by the relative position of bregma, and a slightly more anteriorly placed lambda. The Late Paleolithic specimens also showed a slightly anteriorly, but not superiorly as in Neanderthals, placed glabella relative to the mean configuration for all modern humans, suggesting a relative robusticity of the supraorbital region in this sample. These resemblances between the two fossil samples were minimal and the Late Paleolithic Europeans in no way approached the Neanderthal conditions.

The configurations of the individual Late Paleolithic specimens were also compared to the mean Neanderthal and recent human configurations, as some of these specimens, particularly the Mladec crania, have been proposed by some authors to show stronger similarities to Neanderthals, seen as evidence of continuity or interbreeding with this fossil group (Jelinek, 1969; Vlcek, 1970; Smith, 1982, 1984; Bräuer, 1989; Smith, 1992; Wolpoff, 1992; Churchill and Smith, 2000; Wolpoff et al., 2001). All Late Paleolithic specimens were very similar to the modern human mean configuration and differed from Neanderthals in the same ways as modern humans did. Mladec 5 did show a somewhat lower vault, although not nearly as low as in Neanderthals, and a very anteriorly positioned lambda. In all other aspects, however, this specimen was very similar to the mean modern human configuration. Predmosti 3 and Cro Magnon 1 also exhibited a somewhat low vault and anteriorly placed lambda, but to a lesser degree. This lack of strong morphological similarities, as well as the magnitude of the morphological distance between Neanderthals and Late Paleolithic Europeans, are inconsistent with the predictions of Hypothesis B and do not support claims of contribution of the former to the evolution of early modern Europeans.

The affinities of the Late Paleolithic specimens relative to recent humans are also of interest. Ferembach (1985) has proposed that the Late Paleolithic Europeans originated from the North African Aterians around 50 ka and that a 'Cromagnoid' group, probably an Epigravettian Italian population, gave rise to the Mesolithic populations of Northern Africa, represented here by the Afalou/Taforalt sample. Similarities

between the Late Paleolithic European specimens and the North African Mesolithic material have been noted in the past both from general morphology (Ferembach, 1962; Chamla, 1978; Lahr, 1996) and from multivariate analyses of craniofacial measurements (Bräuer and Rimbach, 1990; Turbón et al., 1997). Here the Late Paleolithic group does cluster with the Epipaleolithic population in the cluster analysis of Step 2. It was found to be closest in Mahalanobis distances to the Melanesian Tolai and Australian populations in Step 1, and to the Austrian Berg and the Epipaleolithic in Step 2. Some similarities between the Late Paleolithic specimens and the Afalou–Tafolalt sample are therefore indicated by this analysis. However, the hypothesis of a close phylogenetic relationship between the two cannot be supported unequivocally based on the measurements and specimens used here.

Neanderthals were found to be widely separated from the two early anatomically modern human specimens included in this analysis, Skhul 5 and Qafzeh 9. These specimens were also very distant from all recent human groups but were relatively close in Mahalanobis D^2 to the Late Paleolithic specimens. They differed from the Neanderthal mean configuration in having a higher vault, a less pronounced supraorbital area and a more posteriorly placed prosthion, features characteristic of modern humans (Fig. 2g–j). However, they differed from the recent human mean configuration in their relatively more anterior placement of glabella and more posterior placement of nasion (marked in Skhul 5, absent in Qafzeh 9), the more inferior position of prosthion, and the more lateral position of the auriculare relative to the glenoid fossa (particularly in Qafzeh 9). These differences suggest a greater robusticity in the supraorbital region, a longer face and a strong supramastoid crest, and are consistent with previous descriptions of these fossils (McCown and Keith, 1939; Vandermeersch, 1981). The very large morphological distances between the early modern humans and recent humans are in keeping with previous metric studies of both cranial and postcranial measurements (Stringer, 1974; Bräuer and Rimbach, 1990; Bräuer, 1992; Kidder et al., 1992; Stringer, 1992; Pearson, 2000). They could be

interpreted as due to their having retained primitive conditions, as has been suggested by Stringer (1992), perhaps related to greater robusticity. However, they are also partly the result of the very small sample size and the poor preservation of these specimens: Qafzeh 9 in particular shows pronounced asymmetry and warping along the sagittal axis.

6. Conclusions

This study developed two models of variation based on the living primate taxa of modern humans and chimpanzees in order to obtain measures of both intra- and inter-specific morphological distances based on three-dimensional coordinates of craniofacial landmarks. These measures were compared to the distances found between Neanderthals and recent human populations, as well as to those between Neanderthals and Late Paleolithic/early modern human samples, so as to help clarify the Neanderthal taxonomic position. Neanderthals are consistently more widely separated from Late Paleolithic Europeans, early anatomically modern humans and recent human groups than either modern human populations or the two chimpanzee species and subspecies are from each other. Although Neanderthals were closest to the Late Paleolithic Europeans in one step of the analysis, they showed a large morphological distance from, and no strong morphological similarities to, this group and to the early anatomically modern human specimens. The two early anatomically modern humans included, Skhul 5 and Qafzeh 9, showed large morphological distances also from recent human populations, but not from the Late Paleolithic group. The great separation between these specimens and recent humans may reflect retention of primitive traits in the former, perhaps related to greater robusticity, but may also be an artifact of their very small sample size and poor preservation. Further investigation of the shape differences between early anatomically modern specimens and recent humans is warranted.

The findings of this study do not support Hypothesis B, that Neanderthals represent a

subspecies of *Homo sapiens* which contributed to the evolution of modern Europeans. Rather, they are more consistent with Hypothesis A, that Neanderthals represent a different species, *H. neanderthalensis*, which had no contribution to the evolution of modern humans in Europe. However, these results should be viewed with caution as support for Hypothesis A is not unequivocal and morphological differentiation among humans may follow a different pattern from that found in chimpanzees. The development of additional models of inter-specific variation, as well as the development of measures of variability in addition to measures of morphological distance, will help to resolve this issue.

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Appendix A. The unbiased Mahalanobis D^2 matrices are reported for the combined human and chimpanzee sample analysis and for the separate human and chimpanzee sample analyses for both steps. Note that all distances reported are significant to the 0.001 level, except: *=significant to the 0.01 level. Labels are as follows: And, Andamanese; Aus, Australian; Brg, Berg; Dgn, Dogon; Epi, Epipaleolithic; Esk, Inugsuk Eskimo; Eur, mixed W. Eurasian; San, Khoisan; Tol, Tolai; Bon, *P. paniscus*; Sch, *P. t. schweinfurthii*; Trg, *P. t. troglodytes*; Nea, Neanderthal; Skh5, Skhul 5; EAM, Skhul 5 and Qafzeh 9; LP, Late Paleolithic.

Mahalanobis D^2

Step 1

Combined human and chimpanzee samples

	And	Aus	Brg	Dgn	Skh5	Epi	Esk	Eur	San	Tol	LP	Bon	Nea	Sch	Trg
And	0.00														
Aus	51.51	0.00													
Brg	50.13	32.72	0.00												
Dgn	26.24	33.64	41.29	0.00											
Skh5	188.18	165.86	165.36	183.26	0.00										
Epi	50.77	42.82	28.27	37.79	149.73	0.00									
Esk	52.15	36.23	38.78	31.73	185.31	37.93	0.00								
Eur	33.64	25.14	9.63	21.98	188.08	24.77	29.32	0.00							
San	61.80	18.65	31.20	29.64	196.19	49.67	33.60	25.23	0.00						
Tol	41.08	12.81	30.79	32.85	158.51	38.03	35.07	23.91	30.39	0.00					
LP	59.72	32.72	39.83	51.27	136.00	43.40	42.47	37.80	40.08	32.46	0.00				
Bon	348.74	304.78	367.01	348.91	439.62	396.27	330.74	357.02	340.49	306.18	328.06	0.00			
Nea	95.61	66.46	86.95	95.28	178.95	100.57	91.39	73.05	90.30	69.50	64.96	254.20	0.00		
Sch	519.66	473.03	550.92	524.88	635.55	592.72	515.57	538.47	518.49	472.32	507.32	58.43	412.28	0.00	
Trg	580.93	538.29	620.00	582.96	702.45	661.42	579.28	606.37	579.22	538.94	578.12	89.12	472.51	10.43	0

Human sample

	And	Aus	Brg	Dgn	Skh5	Epi	Esk	Eur	San	Tol	LP	Nea
And	0.00											
Aus	51.41	0.00										
Brg	51.68	39.66	0.00									
Dgn	27.35	39.37	44.62	0.00								
Skh5	215.34	204.43	186.87	218.63	0.00							
Epi	48.77	50.18	30.92	39.09	174.43	0.00						
Esk	53.11	38.69	38.39	33.40	213.54	37.59	0.00					
Eur	36.54	30.00	10.74	23.95	220.85	29.78	28.49	0.00				
San	58.76	21.78	35.74	29.94	233.72	51.64	36.14	26.06	0.00			
Tol	43.09	13.35	35.51	38.33	196.75	42.67	35.96	28.76	31.15	0.00		
LP	58.82	35.09	47.43	52.00	181.16	47.89	46.21	41.27	42.02	35.03	0.00	
Nea	116.24	79.68	103.66	121.58	222.33	120.59	105.22	89.64	110.80	87.45	75.80	0.00

Chimpanzee sample

	Bon	Sch	Trg
Bon	0.00		
Sch	53.46	0.00	
Trg	69.87	16.32	0.00

Step 2

Combined human and chimpanzee samples

	And	Aus	Brg	Dgn	EAM	Epi	Esk	Eur	San	Tol	LP	Bon	Nea	Sch	Trg
And	0														
Aus	33.46	0													
Brg	23.10	16.40	0												
Dgn	14.24	17.88	22.04	0											
EAM	54.23	54.01	47.32	54.14	0										
Epi	24.39	21.72	15.98	22.29	40.11	0									
Esk	29.33	11.28	15.29	20.47	57.10	22.94	0								
Eur	16.19	10.47	4.72	10.46	52.53	11.46	11.37	0							
San	45.15	8.67	19.63	21.43	58.60	35.45	18.36	17.54	0						
Tol	19.58	7.50	11.43	15.25	55.77	14.62	9.50	6.35	18.49	0					
LP	32.07	17.39	11.68	29.85	24.89*	14.26	19.17	18.32	21.68	16.60	0				
Bon	213.16	187.62	206.47	208.40	233.99	204.68	178.07	204.26	189.90	192.08	194.71	0			
Nea	54.22	38.20	45.28	49.41	48.84	50.01	34.54	42.38	42.84	38.91	36.50	145.32	0		
Sch	264.29	237.63	253.95	259.71	291.96	251.09	224.46	251.50	245.36	239.48	240.24	27.36	174.35	0	
Trg	317.07	287.69	310.60	308.84	333.63	305.45	277.20	306.04	293.41	291.71	293.00	47.26	216.45	8.47	0

Human sample

	And	Aus	Brg	Dgn	EAM	Epi	Esk	Eur	San	Tol	LP	Nea
And	0											
Aus	36.03	0										
Brg	22.62	18.68	0									
Dgn	15.37	20.42	22.83	0								
EAM	53.82	65.18	48.76	57.55	0							
Epi	23.06	26.55	16.74	22.92	40.86	0						
Esk	28.30	14.06	15.46	20.18	62.57	23.57	0					
Eur	16.90	11.50	5.03	11.15	57.53	13.66	11.13	0				
San	46.21	9.34	20.76	23.23	65.54	37.77	19.90	17.56	0			
Tol	21.54	8.46	12.86	18.55	62.15	17.01	10.87	7.86	19.82	0		
LP	30.50	21.54	13.60	29.28	27.00*	14.82	21.20	20.07	24.67	19.60	0	
Nea	58.63	41.28	47.09	52.42	59.62	56.52	40.65	44.69	46.57	44.70	42.95	0

Chimpanzee sample

	Bon	Sch	Trg
Bon	0		
Sch	22.40	0	
Trg	28.18	6.33	0

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