Actes du XIVème Congrès UISPP, Université de Liège,
Belgique, 2-8 septembre 2001

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Belgium, 2-8 September 2001

SECTION 1 : THÉORIES ET MÉTHODES / THEORY AND METHOD

Colloque / Symposium 1.7

Three-Dimensional Imaging in Paleoanthropology and Prehistoric Archaeology

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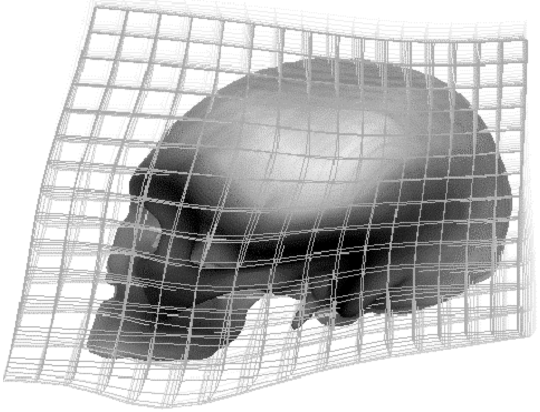

BAR International Series 1049
2002

MODELS OF SHAPE VARIATION BETWEEN AND WITHIN SPECIES AND THE NEANDERTHAL TAXONOMIC POSITION: A 3D GEOMETRIC MORPHOMETRICS APPROACH BASED ON TEMPORAL BONE MORPHOLOGY

Katerina HARVATI

Résumé: La position taxonomique des Néandertaliens est assez controversée. Les espèces fossiles sont souvent définies par comparaison avec des espèces actuelles. Une telle comparaison doit prendre en compte la variation morphologique parmi les populations d'une même espèce, ainsi qu'entre des espèces différentes. Plusieurs caractères Néandertaliens se trouvant sur l'os temporal, deux modèles de variation de la morphologie de l'os temporal ont été développés en utilisant la morphométrie géométrique tridimensionelle. Le premier modèle est basé sur la variation parmi les populations d'hommes modernes, et le deuxième sur la variation parmi les espèces et sous-espèces de chimpanzés. 15 points ont été enregistrés sur l'os temporal de : 12 Néandertaliens, 2 hommes anatomiquement modernes, 4 Européens du Paléolithique supérieur, 2 spécimens du Pléistocène moyen et 270 spécimens de H. sapiens actuel, répresentant 9 populations, chacune de 30 sujets. L'échantillon des chimpanzés comprenait 35 Pan paniscus, 29 Pan t. troglodytes et 30 Pan t. schweinfurthii. Les spécimens ont été superposés en utilisant le logiciel GRF-ND et les méthodes de superposition Procruste (Generalized Procrustes Analysis). Pour la morphologie de l'os temporal, la distance Mahalanobis entre les Néandertaliens et les populations d'hommes modernes est plus grande que celle entre les deux espèces de chimpanzés. Les Néandertaliens ne montrent aucune similitude morphologique avec les Européens du Paléolithique supérieur et les Européens actuels. Bien que les données des populations humaines modernes se recouvrent largement, il existe de nets groupes géographiques.

Abstract: The taxonomic position of Neanderthals is a matter of wide disagreement. Species recognition in paleontology must be based on analogy with living species, in which both intra- and inter-specific morphological variation is assessed. As several traits that characterize Neanderthals are located on the temporal bone, two models of temporal bone variation were developed using 3D geometric morphometrics, based on modern human populations and chimpanzee species and subspecies. 15 temporal bone landmarks were recorded on 12 Neanderthals, 2 early anatomically modern humans, 4 Late Paleolithic Europeans, 2 Middle Pleistocene specimens and 270 recent humans, the latter representing nine populations of 30 individuals each. The chimpanzee sample included 35 Pan paniscus, 29 Pan t. troglodytes and 30 P. t. schweinfurthii. The specimens were superimposed in GRF-ND using Generalized Procrustes Analysis. Neanderthals are more distant in Mahalanobis distance in their temporal bone morphology from any modern human population than the two chimpanzee species are from each other. They do not show similarities to either modern or Late Paleolithic Europeans. Although the modern groups overlap extensively, they do show geographic clustering.

INTRODUCTION

The taxonomic position of Neanderthals and their role in the evolution of modern humans are at the center of one of the most heated debates in paleoanthropology today. Some authors recognize this fossil group as a different species, *H. neanderthalensis*, and see no evidence of a Neanderthal contribution to the evolution of modern humans in Europe (e.g. Stringer et al. 1984; Stringer 1989, 1994; Tattersall 1986). Other researchers, however, see Neanderthals as a subspecies, or population, of *H. sapiens,* which contributed to some degree to the evolution of modern Europeans (Wolpoff 1989, 1992; Wolpoff et al. 2001). Several intermediate positions have also been formulated, including replacement with various degrees of gene flow from Neanderthals (Bräuer 1992; Duarte et al. 1999). Most authors agree that assignment of species taxa in paleontology must be made based on analogy to living biological species that are phylogenetically, geographically and ecologically similar to the fossil organisms studied (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 individual 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 cannot be differentiated on the basis of bony morphology alone (Tattersall 1986, 1993; Kimbel and Rak 1993).

This study focused on the temporal bone, where many proposed Neanderthal traits are located, such as the small mastoid process, large juxtamastoid eminence, elevated position of the external acoustic meatus, robusticity of the zygomatic process and more coronal orientation of the petrotympanic crest (Vallois 1969; Santa Luca 1978; Hublin 1988; Condemi 1992; Elyaqtine 1996). Most of these traits are difficult to measure directly with traditional caliper measurements, and have not been subject to rigorous quantitative analysis. Furthermore, the temporal bone makes part of the basicranium, which is thought to be very conservative and little affected by epigenetic factors (Olson 1981) and that was recently shown by Wood and Lieberman (2001) to exhibit low levels of intraspecific variation, and are thus well-suited to interspecific comparisons. The objectives of this study were two-fold: a) to obtain measures of variation both within and between species and to apply them to a comparison between Neanderthals and modern humans, and, b) to evaluate the proposed Neanderthal traits quantitatively, using geometric morphometrics (Harvati 2001a, b, in review, in prep). The predictions used were formulated based on two hypotheses. Hypothesis A, that Neanderthals represent a different species from modern humans, predicts that the morphological distance between Neanderthals and modern humans would be greater than the morphological distance between two modern human populations. It would also be greater than that between the two chimpanzee subspecies, and it would be equivalent to that between the two chimpanzee species. Furthermore, Neanderthals would not show morphological similarities to the Late Paleolithic and recent European specimens. Hypothesis B, that Neanderthals represent a subspecies of *H. sapiens*, predicts that the morphological distance between Neanderthals and modern humans would be equivalent to that between any two modern human populations, or that between the two chimpanzee subspecies. It would be smaller than that between the two chimpanzee species. Furthermore, Neanderthals may not show affinities to recent Europeans, but they would show similarities to the Late Paleolithic European specimens (Relethford 2001a).

MATERIALS AND METHODS

Two hundred seventy modern human crania were digitized, representing nine populations of 30 individuals each and spanning the extremes of the modern human geographical range (Table 1), following Howells' seminal study (1973, 1989). Ninety four chimpanzee specimens were also measured, representing the two chimpanzee species, *P. troglodytes* and *P. paniscus*, as well as two subspecies of the common chimpanzee, *P. t. troglodytes* and *P. t. schweinfurthii* (Table 1). The fossil sample comprised twelve Neanderthal specimens from Europe and the Near East; the early Neanderthal specimen from Reilingen; the Middle Pleistocene African specimen Kabwe; two early anatomically modern humans from the Near East; and four Late Paleolithic anatomically modern humans from Europe (Table 2). Where the original fossils were unavailable, casts from the Anthropology Department of the American Museum of Natural History were measured.

The data were collected and analyzed using 3-dimensional geometric morphometrics. The use of geometric

Table 1 - List of specimens by population and sex for the modern human and chimpanzee samples.

Group	Male	Female	Undetermined	Total
Modern Humans	143	126	1	270
Andamanese (And. Islands, India)	13	17	---	30
Australians (New S. Wales, S. Aus.)	19	11	---	30
Berg (Austria)	15	15	---	30
Dogon (Mali, West Africa)	15	15	---	30
Epipaleolithic (Morocco, Algeria)	18	12	---	30
Inugsuk (Greenland)	15	15	---	30
European (Egypt, Dalmatia, Greece, Italy, Germany)	17	12	1	30
San-Hottentot (South Africa)	16	14	---	30
Tolai (New Britain, Melanesia)	15	15	---	30
Chimpanzees	52	40	2	94
Pan paniscus (Zaire)	16	19	---	35
Pan t. schweinfurthii (Zaire)	18	12	---	30
Pan t. troglodytes (Zaire, Cameroon)	18	9	2	29

Table 2 - Fossil human specimens included in the analysis.

Neanderthal	Late Paleolithic	Early anat. modern	Middle Pleistocene
Saccopastore 2	Cro Magnon 1 (cast)	Skhul 5	Kabwe
La Chapelle (cast)	Mladec 2	Qafzeh 9	Reilingen
La Ferrassie 1 (cast)	Predmosti 3 (cast)		
Shanidar 1 (cast)	Predmosti 4 (cast)		
Circeo 1			
Amud 1			
La Quina 27			
Gibraltar 1			
Krapina 39-1			
Krapina C			
Spy 1			
Spy 2			

morphometrics presents several advantages over traditional morphometrics: a) the geometric relationships are preserved, b) visualization of shape changes in specimen space are possible, and most importantly, c) geometric morphometrics enables the quantification of features that cannot be measured with traditional caliper measurements and are therefore usually described qualitatively (Rohlf 1990; Rohlf and Marcus 1993; Dean D. 1993; Slice 1996; O'Higgins and Jones 1998).

The data were collected in the form of 3-D landmark coordinates, using the Microscribe 3DX portable digitizer. Minimal reconstruction was allowed during data collection for specimens where very little damage was observed in the area of interest. Fifteen homologous landmarks were collected on the temporal bone (Table 3) and the landmark coordinates were processed using Procrustes Superimposition (Generalized Procrustes Analysis), using GRF-ND and Morpheus (Slice 1992, 1994-1999).

This method optimally superimposes specimens so that the sum of squares of residuals across specimens and landmarks is minimized, and also removes size differences, so that the differences they exhibit are due to 'shape' (Rohlf 1990). Since reflection of right and left side is possible in GRF-ND, it was possible to combine in one sample fossil specimens preserving the temporal bone on different sides. Missing data were further reconstructed by mirror imaging for right-left homologous landmarks.

Figure 1 - Temporal bone landmarks, shown on a modern human skull. While dots represent landmarks, black lines between landmarks are links used for convenience in visualization. A: Lateral view, B: Ventral view.

Table 3 - Landmarks measured on the temporal bone.

Temporal bone landmarks	
1. Asterion	(Steps 1-2)
2. Stylomastoid Foramen	(Steps 1-2)
3. Most medial point of the jugular fossa	(Steps 1-2)
4. Most lateral point of the jugular fossa	(Steps 1-2)
5. Lateral origin of the petro-tympanic crest	(Steps 1-2)
6. Most medial point of the petro-tympanic crest at the level of the carotid canal	(Steps 1-2)
7. Porion	(Steps 1-2)
8. Auriculare	(Steps 1-2)
9. Parietal Notch	(Steps 1-2)
10. Mastoidiale	(Steps 1-2)
11. Most inferior point on the juxtamastoid crest (following Hublin 1978a)	(Steps 1-2)
12. Deepest point of the lateral margin of the articular eminence (root of the articular eminence)	(Steps 1-2)
13. Suture between the temporal and zygomatic bones on the inferior aspect of the zygomatic process	(Step 1)
14. Suture between the temporal and zygomatic bones on the superior aspect of the zygomatic process	(Step 1)
15. Most inferior point on the entoglenoid pyramid	(Steps 1-2)

The fitted coordinate configurations resulting from these procedures are thought to lie in Kendall's shape space (Rohlf 1996), although recently Slice (2001) found that 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, since biological data are restricted in their variation, 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 very strong (correlation 0.9998, root MS error 0.0004), and the statistical analysis was performed on the fitted coordinates themselves. These were analyzed using principal components analysis (PCA), canonical variates analysis (CVA), Mahalanobis D^2, cluster analysis and minimum spanning tree analysis. An analysis of variance (ANOVA) was performed on the PCA scores to determine the significance of population effects along each component.

The analysis proceeded in two steps using different numbers of landmarks, in order to maximize the number of specimens included. The group membership information used in the CVA was population membership rather than species or genus information, so as not to bias the results toward separation of pre-designated species. Furthermore, the Mahalanobis distance matrices obtained were calculated correcting for unequal sample sizes (Sarmiento and Marcus 2000), and were used to produce cluster and minimum spanning trees. Singletons were excluded from the last two analyses, as their distances from other groups may be overestimated.

RESULTS

Principal Components Analysis

In both steps of analysis modern humans and Neanderthals were separated along PC 1 (41.07% of the total variance in step 1, 43.8 % in step 2, Figure 2a). Chimpanzees were also very widely separated from modern humans along this component. The separation between Neanderthals and modern humans was more evident in the second step, where more Neanderthal specimens were included. However, one Neanderthal, Amud 1, consistently fell within the modern human range along this component. All chimpanzee groups were found to be significantly different from all modern human populations along this component, while Neanderthals were significantly different from all chimpanzee and all modern human populations, including the Late Paleolithic and anatomically modern human specimens. PC 1 was most highly influenced by differences in the position of the tip of the mastoid process, the tip of the juxtamastoid eminence, the lateral end of the petrotympanic crest and porion. The shape differences reflected by this component are the larger size of the mastoid process, the more lateral position the juxtamastoid eminence, the more posterior placement of the lateral end of the petrotympanic crest, and the more medial position of porion in humans relative to chimpanzees. The same shape differences characterize Neanderthals relative to modern humans, but to a lesser extent. The position of Amud 1 well within the modern human range probably reflects the large size of the mastoid process in this specimen. Neanderthals were partially separated from modern humans along a few additional principal components, which, however, reflected a much smaller proportion of the total variance. These included PCs 9 and 15 (Step 1) and PC 10 (Step 2). Taken together, the shape differences that they showed include a more lateral placement of auriculare, the more inferior and posterior position of the root of the articular eminence and the more inferior and medial position of the tip of the juxtamastoid eminence in Neanderthals relative to modern humans. A more extensive analysis of the shape differences between modern human and Neanderthal temporal bones is presented elsewhere (Harvati 2001b, in prep).

Canonical Variates Analysis

As in the PCA, the first canonical variate separated modern humans from chimpanzees and Neanderthals from modern humans (Figure 2b). It explained 68.9 % (Step 1) and 68.6 % of the total variance and in both cases it is most highly

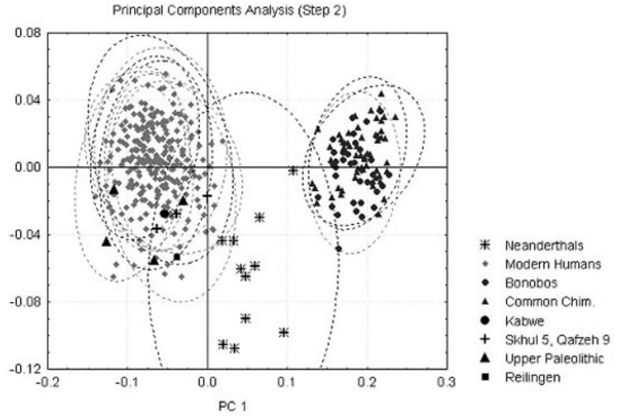

Figure 2 A - Principal Components Analysis (Step 2), PCs 1 and 10.

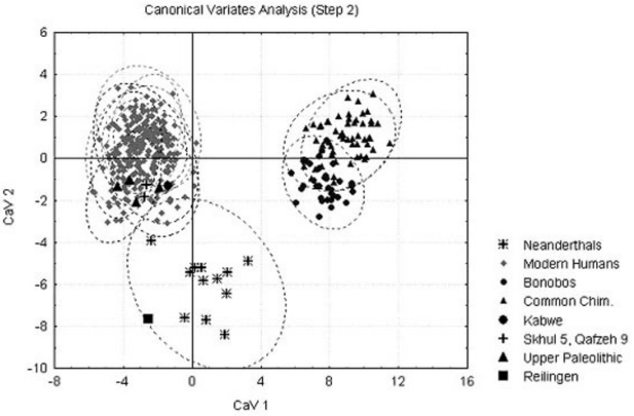

Figure 2 B - Canonical variates analysis (Step 2), CaVs 1 and 2. Dotted lines represent the 95% confidence ellipses for each population.

influenced by PC 1, reflecting similar shape differences to PC 1. Neanderthals were also completely separated from modern humans along CaV 2 (Step 2), which explained 6.5 % of the total variance and was most strongly influenced by PCs 10, 7 and 5.

Mahalanobis D^2, Cluster Analysis and Minimum Spanning Trees

Neanderthals were found to be more distant in Mahalanobis distances from chimpanzees than they are from modern humans. They were more distant from modern humans than the two chimpanzee species and subspecies were from each other. They were also more distant from all modern human groups than any modern human population was from another. The group that was closest to Neanderthals was the Inugsuk Eskimo population. However, the distance between this population and Neanderthals is very large and probably does not indicate any particular morphological affinities. Neither the recent European groups nor the Late Paleolithic European sample, were found to be close to Neanderthals in Mahalanobis distance. Among recent human groups, the three geographic pairs included (Berg and Europeans, San and Dogon, Australian and Tolai) are closest neighbors to each other in both steps of analysis, showing strong geographic clustering. These results were very similar in both Step 1 and 2, and are summarized for Step 2 by the UPGMA analysis and the minimum spanning tree (Figure 3). They are discussed in greater detail elsewhere (Harvati 2001b, in review).

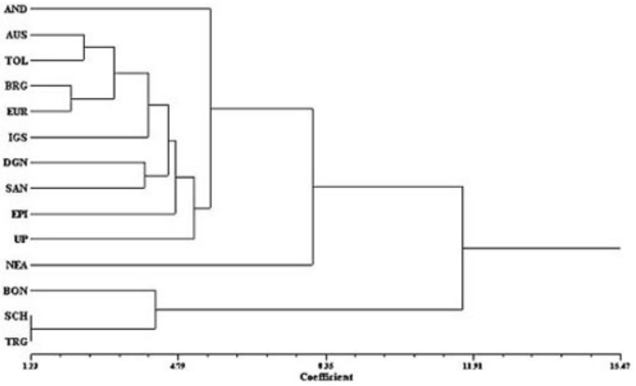

Figure 3 A - Cluster analysis (UPGMA).

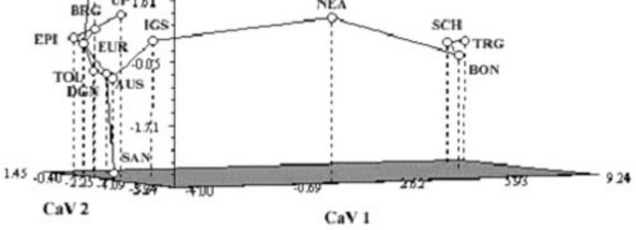

Figure 3 B - Minimum spanning tree (Step 2).

SUMMARY AND CONCLUSIONS

The temporal bone traits measured here were very successful in separating Neanderthals from modern humans, confirming previous qualitative observations. Neanderthals were found to be more distant from modern humans than the two chimpanzee species are from each other, or than any two modern human populations are from each other. Furthermore, they did not show any morphological affinities either to recent Europeans or to the Late Paleolithic European specimens. The morphology of the temporal bone therefore supports the hypothesis that Neanderthals represent a different species from modern humans. Analysis of additional anatomical areas will shed further light on this question.

Acknowledgments

I thank the organizers of this symposium, Bertrand Mafart and Hervé Delingette. I also thank Bill Howells, Chris Stringer, Louise Humphrey, Rob Kruszynski, Yoel Rak, George Koufos, Jakov Radovcic, Henry de Lumley, Marie-Antoinette de Lumley, Dominique Grimaud-Hervé, Gabriella Spedini, Giorgio Manzi, Roberto Macchiarelli, Luca Bondioli, Patrick Semal, the family of Prof. Max Loest, Reinhard Ziegler, Maria Teschler, André Langaney, Mario Chech, Horst Seidler, Sylvia Kirchengast, Niels Lynnerup, Wim van Neer, Ross MacPhee, Ian Tattersall, Gary Sawyer, Ken Mowbray, Eric Delson, Les Marcus, Michelle Singleton, David Reddy and Martin Friess for their help. This research was supported by NSF, the American Museum of Natural History, and the Onassis and CARE Foundations. NYCEP morphometrics contribution No. 6.

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