

Geometric morphometric analysis of mid-sagittal cranial profiles in Neandertals, modern humans, and their ancestors

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Summary - The recent development of geometric morphometrics – and, particularly, the procedures based on the interpolating function thin-plate-spline (TPS) – combine multivariate statistics with deformation grids in the D'Arcy Thompson's style, allowing to distinguish deformation components as well as to explore the variation of the morphological change taken as a whole. Cranial mid-sagittal profiles of fossil specimens referable to the genus Homo, spanning in time from Early to Late Pleistocene have been investigated with this method, with particular reference to the comparison between Neandertals and modern humans. The results show a clear clustering of two main groups, respectively represented by a generalised "archaic" shape and a well characterised "modern" architectural pattern. These results are discussed in the light of a working hypothesis where different archaic Homo lineages represent regional clades of the same anagenetic process of evolution. In contrast, it is suggested that the appearance of modern H. sapiens was a relatively rapid and localised cladogenetic event.

Keywords - Geometric morphometrics, Evolutionary models, Cranium, Neandertals, H. sapiens.

Introduction

Paleoanthropologists, as morphologists, have been always puzzled by the dichotomy between descriptive analysis of the shape (based on visual observations), on one side, and measurements (mainly including inter-point distances) on the other. The development of geometric morphometrics – based on the spatial relationships between landmark points, the proper transformation of these raw data, and the analysis of the transformed data in a multivariate space (e.g., Bookstein, 1991; Rohlf & Marcus, 1993; Marcus et al., 1996) – seems able to shed some light on the issue, providing researchers with a new tool.

Particularly, the analytical procedures based on the interpolating function thin-plate-spline (TPS) – developed, among others, by F.J. Rohlf (1990, 1992, 1993a) on the basis of the theoretical, mathematical, and statistical framework provided by F. Bookstein (e.g., 1991) and other workers (e.g., Goodall, 1983; Kendall, 1984) – describe shape changes as a continuous deformation and combine multivariate techniques with the visualisation of transformation grids in the D'Arcy Thompson's style (1917).

At present, a number of papers dealing with geometric morphometrics have been published and mainly regard within and between species variation as well as systematics and

phylogeny in various invertebrate and vertebrate taxa (see, e.g., various papers in Rohlf & Bookstein, 1990; Marcus et al., 1993, 1996). However, few efforts have been devoted so far to investigate fossil hominids (e.g., Dean, 1993; Yarooh, 1996; Berge, 1996; Bookstein et al., 1999; Lynch et al., 1996; Manzi et al., 1998; Friess, 1998).

In this paper, cranial mid-sagittal profiles of fossil hominines are considered in order to characterise the phenetic variability of this group by multivariate displacement of calvaria shape components, with the aim to contribute in the interpretation of patterns of continuity and discontinuity during the evolution of the genus *Homo*. Attention is focused on the variability between archaic and modern humans, with particular reference to Neandertals and early representatives of *H. sapiens*.

Materials and methods

The mid-sagittal profile represents a useful symmetry plane to describe in two dimensions the architectural morphology of the cranial vault as a whole. Moreover, the curvature of frontal squama and parietals – although it represents a feature based on multiple factors of polygenic and environment-related nature – has been demonstrated to be a trait suitable for phylogenetic analyses (Lieberman, 1995). Such profiles are taken with particular care by paleoanthropologists to document human fossil specimens – thus, they are usually available in the literature to collect a consistent landmark data-set.

Twenty fossil representatives of early modern humans and Neandertals have been considered and are listed in the legend of Figure 1. Selection of specimens was based on the reliability of published profiles and on a criterion of statistical balance between the two morphotypes (N=10+10), aimed to optimise multivariate analyses and output deformation grids. To this basic sample, additional specimens from both Europe and Africa were integrated to represent other archaic (i.e. non-modern) morphs. ER 3733, in particular, was chosen as representative of early *Homo* and regarded as the best available “common ancestor” (Wood 1991; Lieberman 1995). To document the direct Neandertal ancestry, two specimens from Atapuerca Sima de los Huesos was included; similarly, two African crania of the Middle Pleistocene have been selected to compare the range of variability before the appearance of fully modern *H. sapiens* in that continent: Kabwe (Broken Hill) and Jebel Irhoud. In few cases, we were conditioned by the absence of accurate profiles in the literature for specimens to be included in the analysis (i.e. KNM-ER 3733, Kabwe and Irhoud 1); in these cases, data were obtained from contours taken on from first quality casts from the collection of our laboratory. Conversely, photographs and drawings of crania in *norma lateralis* have never been considered, for they both contain various degrees of deformation due to parallax error.

Along the mid-sagittal profile, 18 landmarks ranging from *nasion* to *inion* have been identified in approximately equidistant positions (Tab. 1). We used homologous landmarks as well as “pseudo-landmarks” (geometrically homologous); our set of landmarks thus includes (compare Bookstein, 1991, p. 65): a) Bookstein’s type 1 (juxtaposition of tissues: *nasion*, *bregma*, *lambda*); b) Bookstein’s type 2 (maximum of curvature: *glabella*, *inion*); c) Bookstein’s type 3 (fraction of curvature). Type 3 landmarks, in particular, were obtained as orthogonal projections on the mid-sagittal profile from fixed fractions along the chord between pairs of homologous landmarks. This kind of “pseudo-landmarks” have been preferred to type 2 ones (e.g., metopion, vertex), since they are more clearly identifiable, better represent the development of the curvature in each homologous portion of the cranium, and limit the variation only to radial movements (compare Manzi et al., *in press*).

Two dimensional co-ordinates have been digitised using a graphic tablet. Raw-data have been analysed using a set of TPS-based softwares, developed by F.J. Rohlf (available for downloading at <http://life.bio.sunysb.edu/morph>). The total sample has been previously

checked with TPS-Small (ver.1.17), which allows to know if there could be any bias in shapes statistical comparison due to extreme heterogeneity of the geometries. Then, TPS-Spline (ver.1.15) and TPS-Rel.warps (ver.1.18) have been respectively used for paired comparisons and multivariate statistics on the entire sample.

In the relative warp analysis, the parameter α was settled equal to 1 in order to give importance to large scale variations (e.g., Rohlf, 1993b; Loy et al., 1993); additionally, the entire geometrical variability was also computed setting $\alpha=0$ and including the affine component. TPS-based geometric morphometrics distinguish, in fact, an affine (or “uniform”) component – homogeneously involving the whole configuration of landmarks (e.g., the stretching along a certain axis) – from a non-affine component, which is instead more localised and non-homogeneous. The latter component is further parted according to the so-called *principal warp* – deformations at different geometrical scale which explain the shape variability of the sample. When these principal warps are calibrated to explain the transformation from a reference to a single specimen, they are called *partial warp*. *Partial warp scores* are now the values that characterise each specimen in that partial warp space; together with the affine component, partial warp scores are included in the *weight matrix*, that represents the fundamental source of data submitted to further analyses, including principal components multivariate statistics (*relative warp analysis*).

Tab. 1 - Definition of landmarks.

1	<i>Nasion</i> , meeting point between fronto-nasal sutures
2	Approximation of <i>glabella</i> , as the most protruding point of the supranasal region
3	Orthogonal projection on the mid-sagittal profile of a point at 1/6 of the chord between points 2 and 8
4	Orthogonal projection on the mid-sagittal profile of a point at 1/3 of the chord between points 2 and 8
5	Orthogonal projection on the mid-sagittal profile of a point at 1/2 of the chord between points 2 and 8
6	Orthogonal projection on the mid-sagittal profile of a point at 2/3 of the chord between points 2 and 8
7	Orthogonal projection on the mid-sagittal profile of a point at 5/6 of the chord between points 2 and 8
8	<i>Bregma</i> , meeting point between coronal and sagittal sutures
9	Orthogonal projection on the mid-sagittal profile of a point at 1/6 of the chord between points 8 and 14
10	Orthogonal projection on the mid-sagittal profile of a point at 1/3 of the chord between points 8 and 14
11	Orthogonal projection on the mid-sagittal profile of a point at 1/2 of the chord between points 8 and 14
12	Orthogonal projection on the mid-sagittal profile of a point at 2/3 of the chord between points 8 and 14
13	Orthogonal projection on the mid-sagittal profile of a point at 5/6 of the chord between points 8 and 14
14	<i>Lambda</i> , meeting point between the lambdoid and sagittal sutures
15	Orthogonal projection on the mid-sagittal profile of a point at 1/4 of the chord between points 14 and 18
16	Orthogonal projection on the mid-sagittal profile of a point at 1/2 of the chord between points 14 and 18
17	Orthogonal projection on the mid-sagittal profile of a point at 3/4 of the chord between points 14 and 18
18	Approximation of <i>inion</i> , as the most protruding point of the external occipital protuberance

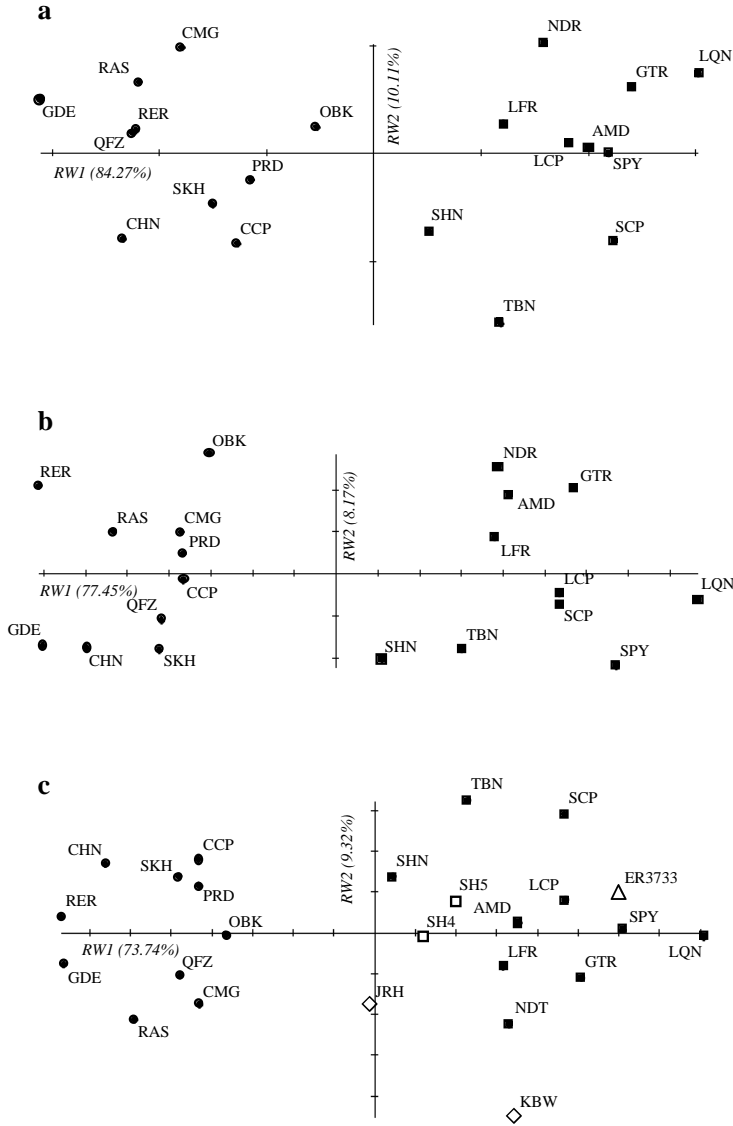


Fig. 1 - Relative warp analysis. **a:** Sample distribution according to first and second RWs with $\alpha = 1$. Specimens are represented by labels and, respectively to taxa, by circles (modern humans) and squares (Neandertals). **b:** Sample distribution according to first and second RWs with $\alpha = 0$ plus affine component included. **c:** Sample distribution according to first and second RWs with $\alpha = 0$ plus affine component, including other archaic morphotypes. Labels - RER: Recent European; RAS: Recent Australian; GDE: Grotte des Enfants 6; OBK: Oberkassel 1; CHN: Chancelade 1; CCP: Combe Capelle 1; CMG: Cro-Magnon 1; PRD: Predmosti 9; QFZ: Qafzeh 9; SKH: Skhül 5; AMD: Amud 1; SHN: Shanidar 1; TBN: Tabun 1; SCP: Saccopasore 1; GTR: Guattari 1; SPY: Spy 1; NDT: Neanderthal 1; LQN: La Quina 5; LFR: La Ferrassie 1; LCP: La Chapelle-aux-Saints; SH4: Sima de los Huesos 4; SH5: Sima de los Huesos 5; JRH: Jebel Irhoud 1; KBW: Kabwe; ER 3733: KNM-ER 3733.

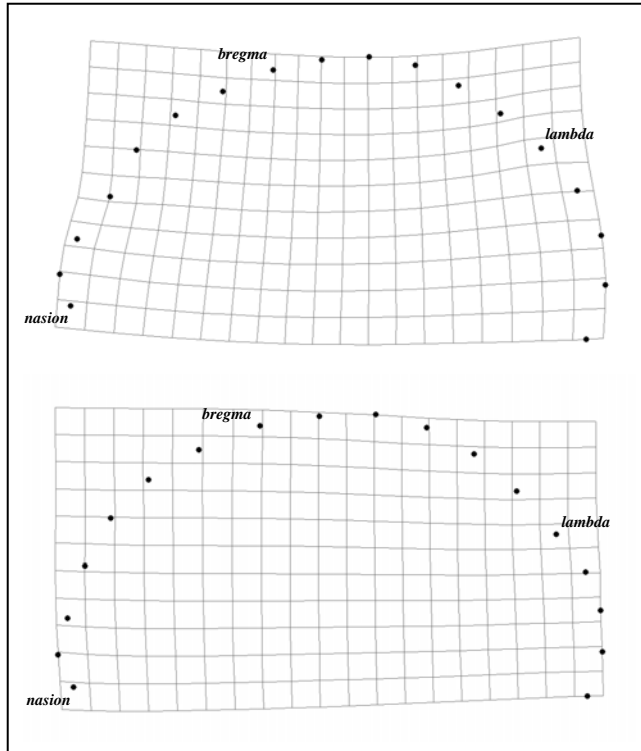


Fig. 2 - Distortion grids in the D'Arcy Thompson's style of positive extreme of RW1 (above) and RW2 (below) in the relative warp analysis of Figure 1a.

Cluster analysis was computed by UPGMA using the Phylogeny Inference Package (PHYLIP, version 3.57c; Felsenstein, 1989), while phenograms are computed with TREEVIEW (Page, 1996).

Results

The distribution of the sample (Neandertal and modern specimens only) according to the first and second principal components of the relative warp analysis, performed for $\alpha=1$ (non-affine variation only), is reported in Figure 1a. The first and second principal components, or relative warps (RWs), explain together 94.4% of the total variance. Two clearly separated groups result isolated, respectively representing a modern pole and an archaic (Neandertal) one. No inter-group superimposition occurs, and the amount of intra-group variation among the subsamples is rather comparable; early members of the modern morphotype, as Skhûl 5 and Qafzeh 9, are well settled inside the modern range of variability.

The first RW explains the greatest part of the total variance (84,3%), representing the axis of morphological discontinuity between the two morphotypes. If we use the TPS interpolant function to display shape differences along the RW1 axis (moving from the modern range towards the archaic one; see Fig. 2a), we observe a general contraction of the

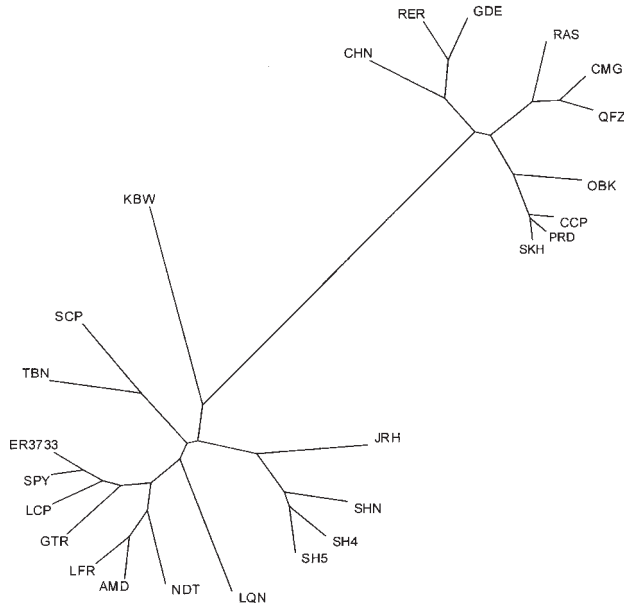


Fig. 3 - Phenogram based on UPGMA of a distance matrix calculated from RW1 and RW2 values with $\alpha = 0$ (for labels see Fig.1).

vault, particularly involving the frontal squama and the parietal mid-sagittal profile, associated to enlargement of the supraorbital torus and outward extension of the occipital squama. The second RW captures further intra-group variation, and explains 10,1% of total variance. As shown in Figure 2b (toward the positive limit of the scores) it involves a light enlargement of the fronto-parietal components and a comparable decline of the posterior vault (parieto-occipital). This axis of variation seems mainly related to individual architectural features, probably in relationship with other districts of the cranium (face and base).

Re-processing the relative warp analysis for $\alpha=0$ and the affine component included (Fig. 1b), the first and second RWs explain together 85,6% of the total variation. The two morphotypes are now separated by a larger gap than that observed in the previous analysis (Fig. 1a); at the same time, the modern specimens appear more grouped than the Neandertals.

The inclusion of the entire degree of variation registered by TPS ($\alpha=0$ plus affine) should be regarded as more consistent with the actual morphological variability, since it is well known that great part of the diversity between a human archaic cranial vault and a modern one is related to platicephaly, that is to a uniform deformation from an elongated shape to a more rounded one or vice versa. Therefore, this same setting of analytical parameters has been applied to the entire sample, including also early *Homo* and Middle Pleistocene specimens from Africa and Europe (Fig. 1c); consistent results are however obtained also for $\alpha=1$ (where the affine component is not included). In this case, the first two RWs explains together 83,1% of the total variability. What is immediately apparent is that all the archaic specimens group together, within the same range of variability of the Neandertals (at least for the 1st RW), and that the same bimodal pattern previously observed can be further identified. As a matter of fact, while one pole is always represented by the modern morphotype, the other one represents now a general archaic morph that apparently includes

different taxa of the genus *Homo*, without a clear separation in terms of chronology and/or chorology. Sima de los Huesos crania and the ancestral reference ER 3733 are definitely inside the Neandertal range in this analysis, while African specimens of the late Middle Pleistocene, as Kabwe and Irhoud, stay in a peripheral position compared to the core of the archaic variability observed here (Neandertals and Anteneandertals plus ER 3733).

In general, all the analyses presented above (Figs 1 a-c) show that the morphological diversity between the archaic and the modern shape (i.e., “form” without size of the mid-sagittal profile of the cranial vault) is represented as a clear gap by TPS. In order to demonstrate the bimodal nature of the distribution obtained, a phenogram was computed on the distances between specimens inside the multivariate morphospace derived from the relative warp analysis in Figure 1c. The phenogram reported in Figure 3 confirms the existence of two discrete entities: the *modern* cluster – that includes all the specimens commonly assigned to *H. sapiens* – clearly opposed to the *archaic* one. The latter group results less homogeneous than the former, yet well defined, and composed by three subgroups: a) a main cluster including all the Neandertals plus ER 3733; b) a lesser cluster with some “transitional” specimens from Europe (Sima de los Huesos), Africa (Irhoud), and the Near East (Shanidar); and a third one (c), with only the African Middle Pleistocene fossil from Kabwe.

In this light, a direct comparison was computed operating a spline from the ancestral reference (ER 3733) to specimens – such as Guattari, Kabwe, Irhoud, and Cro-Magnon – respectively representing the main branches obtained. Affine, and non-affine components of these shape variations are shown in Figure 4.

ER 3733 vs Guattari (Fig. 4a). The affine component involves a longitudinal stretching resulting in forward displacement of both supraorbital torus and occipital squama, associated to a backward inclination of the biparietal profile. The non-affine component is concentrated in the frontal region, where a different development of the torus and a different profile of the squama are well described by the spline, as well as in the occipital region, where lambdoid flattening and bun formation can be observed.

ER 3733 vs Kabwe (Fig. 4b). The affine component describes a stretching very similar to that observed above for Guattari; conversely, the non-affine warp shows lesser bending of the frontal squama, enlargement of the fronto-parietal curvature, depression along the entire parieto-occipital profile (absence of bunning).

ER 3733 vs Irhoud (Fig. 4c). While the affine component is rather comparable with the distortion from the ancestral reference to other archaic specimens (see above), it reveals also a different fronto-parietal profile (absence of backward inclination). At the same time, the non-affine component appears similar to the warp toward modern humans (see below), representing a “bridge” between the pattern observed in Kabwe and that shown by Cro-Magnon.

ER 3733 vs Cro-Magnon (Fig. 4d). The affine component obviously reflects the vertical stretching expected in the comparison between low and high vaults, associated to an uniform relative shortening of the cranium in antero-posterior direction. The non-affine component shows marked browridge reduction, frontal squama enlargement, different contour of the biparietal vault, and more rounded occipital.

Discussion

This multivariate analysis of the shape of the human cranial vault has distinguished two different and discontinuous morphological patterns within the genus *Homo* – one common to various non-modern taxa (*H. ergaster*, *H. heidelbergensis*, *H. rhodesiensis*, *H. neanderthalensis*) and a derived one associated with *H. sapiens*.

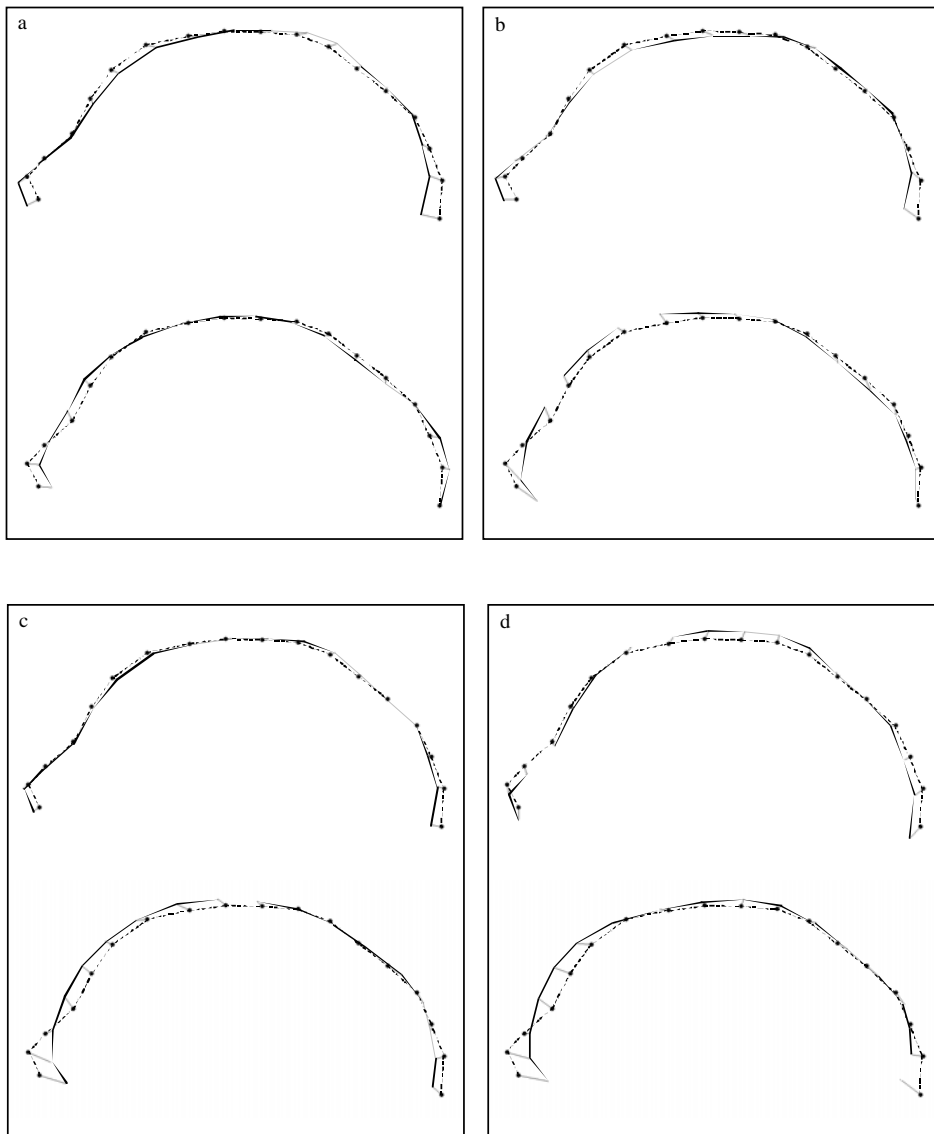


Fig. 4 – Vectorial resolution of the affine (above) and non-affine (below) components of the TPS transformation between: a) ER 3733 vs Guattari; b) ER 3733 vs Kabwe; c) ER 3733 vs Irhoud; d) ER 3733 vs Cro-Magnon.

The mid-sagittal profile of the cranial vault is a complex phenetic trait regarded as a useful feature to identify and characterise different phenotypes with suggested phylogenetic value (Lieberman 1995). Moreover, since the architecture of the cranial vault is a complex character – related to a polygenic, epigenetic, and multifactorial background – it is likely to be hypothesised a pattern of continuous and gradual variability between related populations, ultimately sharing the same gene-pool. On the basis of the present TPS analysis, however, there is no phenetic continuity between two distinct morphotypes. The human variability considered here, in fact, shows a clear bimodal pattern between a *modern* pole and an *archaic* one, as demonstrated by both multivariate statistics (Fig. 1 a-c) and cluster analysis of such a multivariate shape (Fig. 3).

This obviously reflects “platicephaly” – a well known plesiomorphic feature shared by all the archaic humans (Neandertals included). It is described here by the non-affine deformations mainly acting on both the frontal and occipital regions, plus an affine component characterised by longitudinal stretching and intermediate contraction. It seems to us that neither multivariate statistics based on traditional metric data (e.g., Stringer, 1974; Howells, 1989; Arsuaga et al., 1997) nor other geometric morphometrics approaches to the issue (e.g., Yarooh, 1996) were able to discriminate so clearly for this complex trait. The exception is represented by another TPS-based work (Friess 1998), where – using photographs in lateral view of a far rich recent human sample compared to anatomically modern and archaic fossil crania – a basic separation “entre crâne à morphologie moderne et crâne à morphologie archaïque” (p. 259) is observed. Similar results are also obtained applying the Fourier analysis to these same profiles (e.g., Pesce Delfino et al., 1991).

In this respect, it must be stressed the importance of geometric morphometrics in analysing shape directly (as spatial relationships between landmark points), and to virtually eliminate the size component. After GLS superimposition (performed by the TPS-based softwares as an appropriate re-scaling and alignment system), the first principal component is almost size free, although it possibly contains some residual size-related information due to allometry (Bruner & Manzi, 2000).

However, in a comparison between the vault architecture of Neandertals and modern humans, it is conversely probable that size plays a negligible role, since both morphotypes reach similar values of cranial capacity (viewed as a measure of size for the braincase). The morphological discontinuity between Neandertals and modern humans observed on the 1st principal component, or RW1 (explaining always the great majority of the total variance: 84.3%, 77.5%, and 73.7% respectively in different analyses; compare Fig. 1 a-c), does not provide support to theories involving an effective genetic interaction (e.g., Frayer et al., 1993). On the contrary, it supports hypotheses where distinct evolutionary events (or processes) are assumed for the two morphotypes, as in the single-origin model for modern human variability (e.g., Stringer & McKie 1996). Furthermore, adding the range of variation along the 2nd principal component (RW2 in Fig. 1 a-c), a comparable rank for the two taxa emerges, suggesting the idea of distinct and equivalent “morphological niches” for each of them, as far as the mid-sagittal profile of the cranial vault is concerned.

Including other specimens in the analysis – the ancestral reference, represented by the Plio-Pleistocene African ER 3733, and some Middle Pleistocene crania from Africa (Kabwe and Irhoud) and Europe (Sima de los Huesos crania 4 and 5) – we clearly observe that all these fossils are well settled inside the archaic variability. This suggests that, at phenetic level – or even at phylogenetic level, whether such a value is assumed for mid-sagittal vault profiles – all these archaic morphotypes belong to a continuous and gradual (i.e. anagenetic) radiation, where a single biological model is represented by different variants. On the other hand, the modern profile seems to be the result of a basically different pattern, belonging to an independent radiation. The specimen in our sample which are supposed to be

phylogenetically related to the origin of modern humans, particularly the late Middle Pleistocene African Irhoud 1, does not seem to have still trespassed that organisation threshold and clearly cluster with the non-modern morphotype. It is puzzling, however, that Irhoud shows an “archaic” affine warp associated with a “modern” non-affine one (Fig. 4d), facing the uncertain position of this debated specimen in cladistic analyses (e.g., Stringer, 1974). It is also of interest that, despite the extraordinary diversity in the morphology of the frontal torus between Kabwe and Irhoud, these two Middle Pleistocene Africans are very similar in the mid-sagittal braincase profile (compare Figs 4c and 4d), showing also affinities with both ER 3733 (from one side) and Cro-Magnon (from the other). At the same time, it was expected that Near Eastern Middle Paleolithic specimens, like Qafzeh 9 and Skhül 5, are completely modern also from the architectural point of view described here.

It can be concluded that by using geometric morphometrics to discriminate different phenotypic patterns we are able to support the idea that Neandertals and modern humans were respectively the result of two different evolutionary trajectories, as already indicated by different sources of data, including traditional morphometrics (Howells, 1989; Stringer, 1974, 1996), distance matrices (Waddle, 1994), and mitochondrial DNA (Krings et al., 1997). Stringer already suggested that Neandertals have a contrary relationship in size and shape comparing the face and the cranial vault (e.g., Stringer, 1994). As far as the cranial vault is concerned, Neandertals are indeed most like enlarged archaic humans in the cranial vault (size predominates), whereas among modern humans the cranial vault is also reshaped (shape predominates). Our comment is that the clear fitting of the Neandertals inside a generalised archaic cluster (including the assumed common ancestor) confirms that non-modern variability is the result of an anagenetic radiation, based on evolutionary variants from a single model – a sequence of chronospecies according to Arsuaga and co-workers (1997) as far as the European case-study is concerned – while modern variability is more probably the result of an African, rapid, and localised cladogenetic event (compare Manzi, 2000).

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ABSTRACT

Analisi di morfometria geometrica del profilo sagittale del cranio nel Neandertal, nell'uomo moderno e in forme umane ad esse ancestrali

Riassunto - Il recente sviluppo della morfometria geometrica - e in particolare delle procedure basate sulla funzione interpolante *thin-plate-spline* (TPS) - integra l'analisi delle griglie di distorsione di D'Arcy Thompson con la statistica multivariata. Tramite la scomposizione vettoriale della geometria complessiva questo approccio permette una trattazione quantitativa della variabilità morfologica. Sono stati analizzati profili cranici medio-sagittali di campioni fossili riferiti al genere *Homo*, distribuiti in un arco temporale

che va dal Pleistocene inferiore al Pleistocene superiore, con riferimento particolare al confronto tra neandertaliani e uomini anatomicamente moderni. I risultati mostrano un netto *clustering* di due gruppi principali, rappresentati rispettivamente da una forma “arcaica” e da un modello strutturale “moderno”. I risultati vengono discussi alla luce dell’ipotesi secondo la quale le differenti linee evolutive arcaiche del genere *Homo* rappresentino distinti morfotipi regionali, risultato di un comune processo evolutivo anagenetico. Al contrario, viene proposto che la caratterizzazione evolutiva dell’uomo anatomicamente moderno sia stato il risultato di un evento cladogenetico discreto e localizzato.

Parole chiave - Morfometria geometrica, Modelli evuzionistici, Cranio, Neandertal, *H. sapiens*.

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