

# Midsagittal Cranial Shape Variation in the Genus *Homo* by Geometric Morphometrics

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## ABSTRACT

*Midsagittal profiles of crania referred to different taxa of the genus Homo have been analyzed by geometric morphometric techniques. Comparisons between single specimens using the thin-plate-spline function suggest a generalized reduction of the lower face, associated with antero-posterior development of the braincase occurring (possibly in parallel evolution) along distinct human lineages. Furthermore, Neandertals display a projection of the midface, and modern humans show a derived globularity of the vault associated with midsagittal parietal bulging. Principal Component Analysis demonstrates a bimodal pattern of variation, which describes an »archaic« pole (rather heterogeneous in terms of taxonomy) clearly distinguishable from the modern one. The first two principal components – that explain together 80% of the total variance in shape – involve respectively fronto-parietal expansion and midfacial prognathism. These results contribute to identify different structural patterns in human evolution, supporting discontinuity rather than continuity of cranial shape among different taxa of the genus Homo, especially when considering the differences between Neandertals and early modern humans.*

**Key words:** cranial shape, geometric morphometry, genus *Homo*

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## New Perspective in Morphometrics

The human cranium is an extremely complex 3D object – the result of a composite functional system. Several factors are involved in its morphology, such as

genetic and physiological adaptations, physical constraints, heredity and stochastic processes. Thus, the interpretation of evolutionary patterns may be easily misdi-

rected by a number of epigenetic factors. However, cranial morphology (in all its components) still represents the best source of phenotypic information we have to analyze human variability, particularly in diachronic comparisons between extinct species and present variation.

During the last couple of decades, the development of new conceptual models and analytical tools, together with the introduction of computer-assisted techniques, moved morphometrics towards a synthetic approach which is based on multivariate analysis of landmark coordinates<sup>1,2</sup>. In the present paper, we study the variability of midsagittal cranial profile within the genus *Homo*, using this geometric morphometric approach. Our aim is to characterize general trends of morphological variation in human evolution and to establish affinities between different morphotypes, moving from a qualitative description of shape variation to quantitative analytical evidence.

### Fossils and Data Sampling

Specimens were chosen in order to include much of the diachronic variability of the genus *Homo*, ranging from Late Pliocene African hominids up to anatomically modern humans. Neandertal variability is particularly well represented, in order to better understand evolutionary dynamics in Europe. External to the genus *Homo*, the best preserved cranium referred to *Australopithecus africanus*, Sterkfontein 5 (Sts 5), was chosen as a reference outgroup.

Two-dimensional midsagittal cranial profiles were considered. The profile of the cranial vault (frontal squama shape and angle, vault curvature, supratatorial sulcus, occipital shape) meets most of the criteria requested in a phylogenetic analysis, namely: homology, polarity (derivation), and a comparable presence in the whole sample<sup>3</sup>. Profiles were sampled

from the literature (published outlines in the original detailed report of each specimen) and monitored on first quality casts available in 1998 from the collection of the Museum of Anthropology at »La Sapienza« University (Rome). Drawings and photos of crania in *norma lateralis* have never been considered, for they include – especially for the cranial vault profiles – various degrees of deformation due to parallax distortion.

Along the midsagittal profile, 10 landmarks ranging from *prostion* to *inion* have been identified in approximately equidistant positions including Bookstein's type 1 (»homologous«, juxtaposition of tissues), type 2 (maximum of curvature), and type 3 (fraction of curvature<sup>4</sup>). Two dimensional coordinates have been digitized using a graphic tablet and the DS-Digit software. The composition of the sample and the configuration of landmarks are reported in Figure 1.

Landmark coordinates have been analyzed by a geometric morphometric multivariate approach<sup>2,4-7</sup>, using TPS software developed by F.J. Rohlf (available at <http://life.bio.sunysb.edu/morph>) and the APS package developed by X. Penin (available at <http://www.cpod.com/monoweb/aps>).

Coordinates systems are superimposed by Generalized Procrustes Analysis, by translation to a common centroid, scaling to unitary centroid size and rotation by least-squared approximation. *Shape* is therefore splitted from *size*, and these two components can be analyzed separately. Residual differences between coordinates are then used for multivariate statistics and inferences. Alternatively, the coordinate systems have been compared by Bookstein superimposition, aligning the configurations to a common baseline. In this comparison, the specimens have been superimposed using *nasion* and the most posterior landmark of the vault as reference points, to optimize the separation

<i>Specimen</i>	<i>Label</i>
Sterkfontein 5	STS5
KNM-ER 1813	ER1813
KNM-ER 3733	ER3733
Zhoukoudian XI	ZKD
Kabwe 1	KBW
Sima de los Huesos 5	SH5
Saccopastore 1	SCP
Guattani 1	GTR
La Ferrassie 1	LFR
La Chapelle a. S. 1	LCP
Amud 1	AMD
Shanidar 1	SHN
Tabun 1	TBN
Irhoud 1	JHR
Skhul 5	SKH
Qafzeh 9	QFZ
Cro-Magnon 1	CMG
Chancelade 1	CHN
Fonterossi	FTR

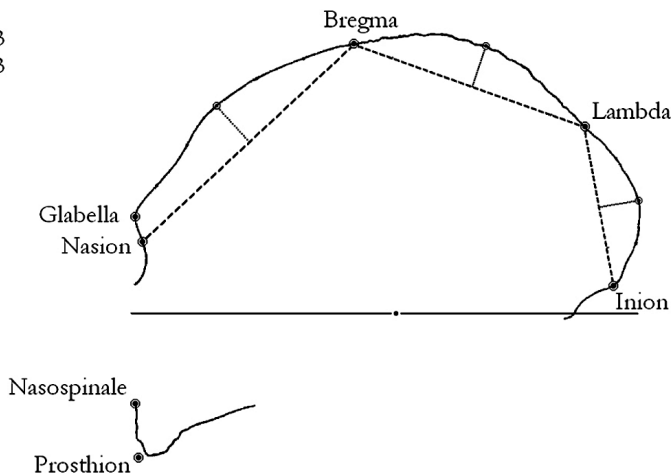


Fig. 1. Specimens (with respective labels) and landmarks along the midsagittal profile used in this study. Orthogonal projections on frontal, parietal, and occipital squama have been taken on the outline at 50% of the cords between homologous landmarks. Note that the specimen from Zhoukoudian is based on the reconstruction by F. Weidenreich (calvaria XI and associated fragments).

between neurocranial and facial structures. Thin-plate spline interpolant function allows a direct visualization of shape changes into the multivariate morphospace, by vector displacement or grids deformation. The unweighted pair-group method using arithmetic averages procedure (UPGMA) based on the procrustes distances matrix has been used to compare the phenetic affinity between the specimens, using tpsSmall 1.19 by F.J. Rohlf, and SynTax 2000 by J. Podani.

Using tpsRegr 1.24 by J.F. Rohlf, shape vectors have been regressed onto cranial capacity values. In fact, centroid size was not available for this purpose, because the midsagittal profiles were not to always at scale. A shape vector was computed by partial least square regression, using tpsPLS 1.11 developed by J.F. Rohlf, and regressed onto the chronology of the specimens to check the morphological patterns through time.

## Results

### *Pairwise shapes comparisons and phenetic clustering*

Considering the overall morphological affinity/divergence between specimens (as residual differences in shape after the superimposition of the coordinates systems), the UPGMA clusters all the anatomically modern crania in a single group, including the early modern specimens from Skhul and Qafzeh, as well as the more controversial Irhoud 1 (Figure 2). The non-modern group is further characterized by the separation of Sts 5 with KNM-ER 1813 from samples of archaic *Homo*. Among them, Neandertals and their European precursors (Atapuerca – Sima de los Huesos, Saccopastore) are clustered together, close to a more generalized group including KNM-ER 3733, Zhoukoudian XI, and Kabwe.

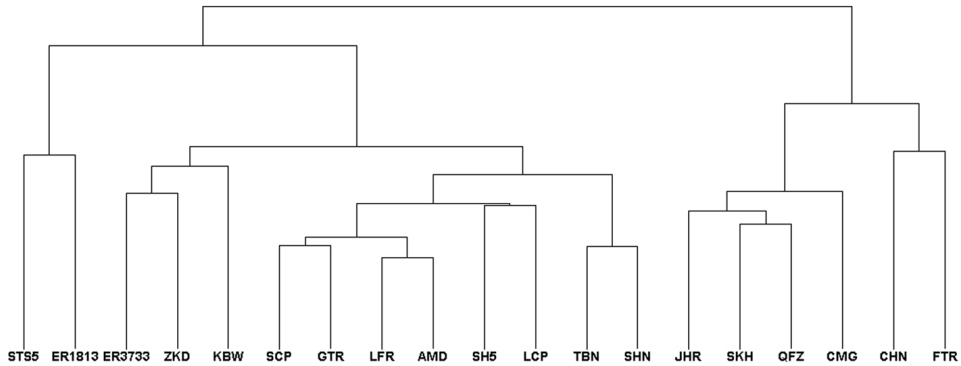


Fig. 2. Phenogram showing the geometric affinities within the sample, computed by UPGMA based on the Procrustes distance matrix (cophenetic correlation coefficient = 0.73).

The thin-plate-spline function<sup>8</sup> can be used to visualize transformations from one landmark configuration to another, warping shapes by minimum energy paths. Four specimens have been used for a pairwise comparison: 1) Sts 5 has been used as outgroup; 2) KNM-ER 3733, which is referred to as early *Homo*, or *Homo ergaster*, was interpreted as an ideal reference for the common ancestor of all the morphotypes included in our genus<sup>3,9</sup>; 3) the cranium from Grotta Guattari (Monte Circeo), has been chosen to represent the »classic« Neandertals<sup>10,11</sup>; 4) the Fonterossi cranium, dated to about 6.5 Ka<sup>12</sup>, has been taken as a good example of the modern human shape.

Both the Procrustes (PS) and Bookstein (BS) superimpositions show similar grid warps, but some differences in single areas can be recognized.

*Sts 5 vs. KNM-ER 3733* (Figure 3a) – Clearly, the more evident distortion is related to a marked reduction and shortening of the face. In the BS, the neurocranium is more flattened when compared to its length, while in the PS the neurocranium shows a frontal heightening and anterior development of the upper face (supraorbital torus), relative to the overall midsagittal size. The grids show

in both cases the development of the occipital areas.

*Sts 5 vs. Guattari* (Figure 3b) – The pattern of vector displacements is similar to the previous comparison (vector displaced with the same orientation and direction), but rather more emphasized. In addition, *prosthion* is more backward shifted than *nasospinale*, involving a further alveolar shortening. This process, together with the anterior development of the supraorbital structures, involves the projection of the midface. Interestingly, even if the magnitude of the pattern is stressed, the comparison between the superimposed profiles of the vault is analogous.

*Sts 5 vs. Fonterossi* (Figure 3c) – The facial reduction and shortening is extremely pronounced, as is the posterior vault development. In contrast, both BS and PS show an extreme globular development of the vault, rather vertical in the former analysis, slightly shifted anteriorly in the latter. In the face, orthognathism is not linked to midfacial protrusion.

Similar results are obtained when KNM-ER 3733 is compared with Guattari and Fonterossi profiles respectively (Figure 4). In the former comparison, the differences are localized in the midfacial

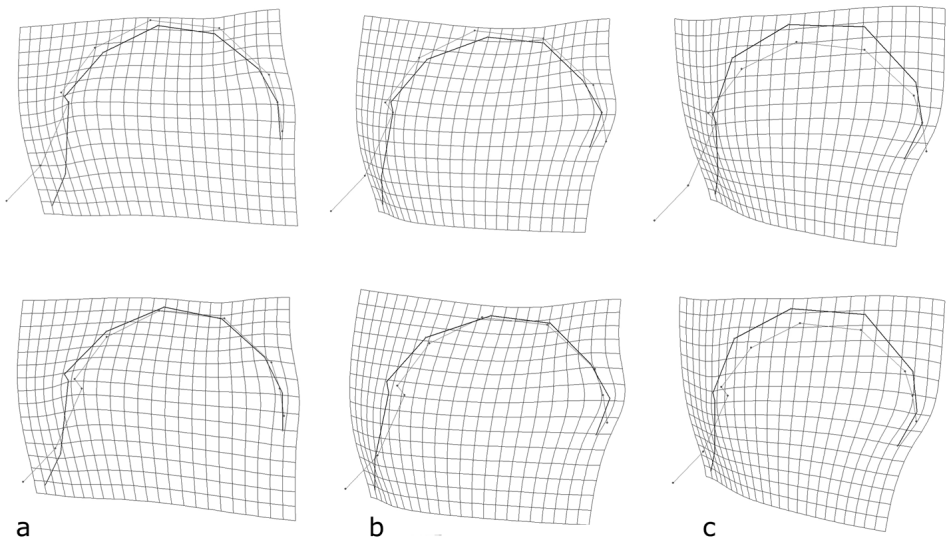


Fig. 3. Pairwise comparisons (target shape in bold), represented by the *Sts 5* midsagittal profile versus KNM-ER 3733 (a), Guattari (b), and Fonterossi (c) respectively. Both Bookstein (top) and Procrustes (bottom) superimposition methods are shown.

protrusion and occipital development (by forward retreat at the *inion*), with minor changes in the vault shape. The midfacial and the occipital development involve a general upward bending of the vault profile, rotating their respective axis away from the cranial base. In the latter comparison, the lower face is extremely reduced, the vault develops vertically, with the bulging of the parietal areas. As a consequence of the facial reduction and vault globularity, the respective axes of

the two cranial districts are rotated with respect to the cranial base.

Some general inferences can be immediately argued. These results are generally in accordance with traditional multivariate approaches to the issue<sup>13</sup>, but the following information is added: 1) size is removed from analyses based on this approach, providing the opportunity to exclude the incidence of this component (usually loading on the first principal component); 2) a direct visual inspection

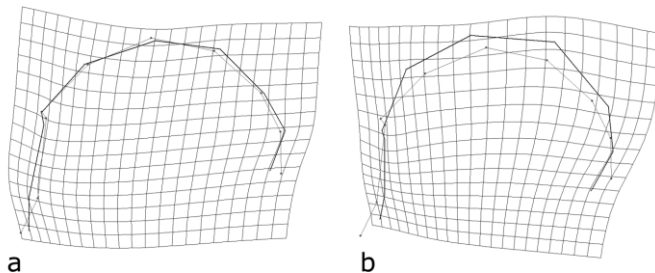


Fig. 4. Pairwise comparisons (Procrustes superimposition, target shape in bold): KNM-ER 3733 midsagittal profile versus Guattari (a) and Fonterossi (b) respectively.

of the morphological change involved is constantly available; 3) the pattern observed is unambiguous.

The warps from the outgroup (the *Australopithecus* specimen from Sterkfontein, Sts 5) towards *Homo* representatives show some general patterns and specific trends. In general, facial volumes decrease moving from *Homo ergaster* to *Homo neanderthalensis* and *Homo sapiens*. Compared with Sts5, the Neandertal morphotype shares with early *Homo* a plesiomorphic structure of the vault (platycephaly, occipital protrusion, and supra-orbital torus development), but shows a peculiarly derived trait in the structural design of the face – the *prosthion* is relatively more retreated than the *nasospinale*, thus the midfacial area is bent forward describing the autapomorphic configuration that is commonly referred to as midfacial prognathism<sup>14</sup>. Conversely, the

modern morphotype shares with early *Homo* the facial pattern, varying only in the degree of expression of the same pattern. In contrast, *Homo sapiens* shows a different (i.e. derived) architecture of the cranial vault, mainly based on the fronto-parietal expansion and on a different curvature of the occipital squama. In this perspective, the peculiar modern development of midsagittal profile of the cranial vault has to be regarded as autapomorphic.

Despite these pairwise comparisons do not take into account the respective intraspecific variability, the observed differences between *Homo ergaster*, *Homo neanderthalensis*, and *Homo sapiens* appear clearly described, largely exceeding variation at the individual level.

#### Relative Warp analysis

In Figure 5 the whole sample is plotted in the shape space described by the

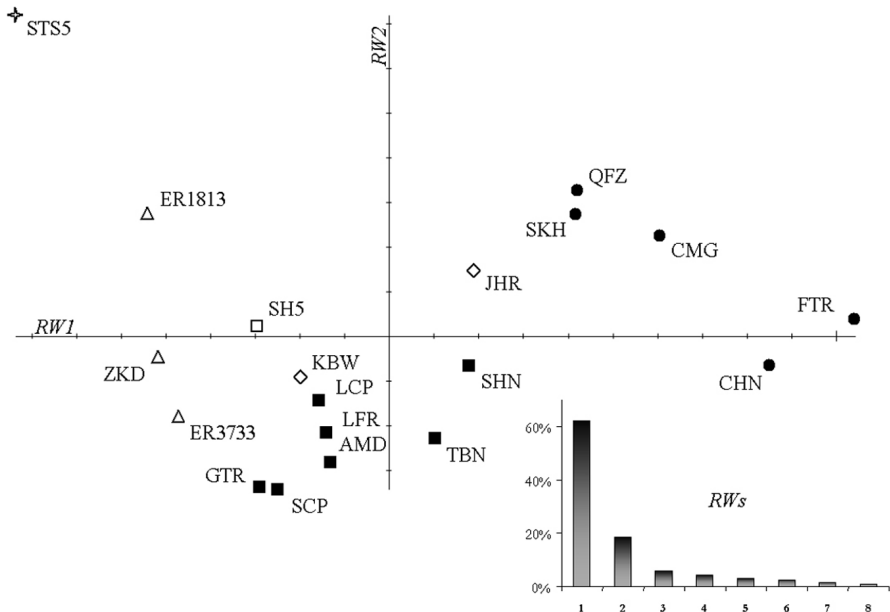


Fig. 5. Principal Component analysis: specimens are plotted in the space described by the first two PCs or Relative Warps (RWs);  $\alpha = 0$ , affine component included. The histogram shows the percentage of variance explained by the first eight RWs.

first two Relative Warps (i.e., principal components), that represent together 80% of the total variance. Here, the phenetic variability for the midsagittal cranial profile in the genus *Homo* appears clearly polarized, with the distinction between an archaic group and a modern one. The first group includes the *Homo ergaster/erectus* cluster, the Afro-European Middle Pleistocene variability and the Neanderthals. The second group refers only to both the early and recent variation of *Homo sapiens*, with the possible inclusion of the

»transitional« Irhoud 1 cranium and some affinity with the Near Eastern Neanderthals. It should be also noted that the modern cluster is approximately as heterogeneous as the archaic one, and that early modern specimens (Skhul/ Qafzeh and Cro-Magnon) are considerably distinct in shape from the relatively more recent crania (Chancelade and Fonterossi).

The first principal component (RW1 = 62% of variance) sets the sample along an archaic-modern axis, explaining most of the differences already observed in the

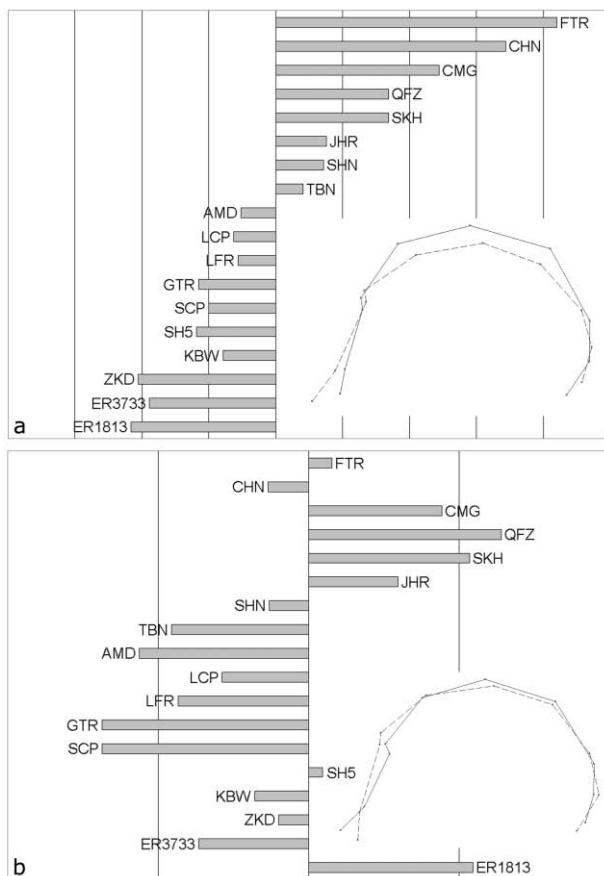


Fig. 6. Specimens' scores along RW1 (a) and RW2 (b); midsagittal shape variations from minimum (dotted line) to maximum (solid line) values are also shown. Specimens are ordered according to taxa; Sts 5 is not reported.

pairwise comparisons. In Figure 6a, the RW1 values for each specimen are reported, and both directions of the distortion involved are represented by displacement of extreme profiles. This component must be related to main determinants in the evolution of the cranium within the genus *Homo*. Particularly, it involves: 1) fronto-parietal growth (vault vertical elevation); 2) orthognathism (reduction of the maxillary profile); 3) changes in the curvature pattern and degree of the occipital squama (with the *inion* moving forward and downward).

The second axis (RW2 = 18% of variance), in turn, mainly accounts for presence/absence of upper and midfacial protrusion, bregma elevation, and occipital projection (see Figure 6b). Therefore, it obviously does not separate archaic morphotypes from the modern ones (compare Figure 5), while it clearly isolates the Neandertal sample in association with some other specimens (KNM-ER 3733 in

particular) that show midfacial protrusion matched by supraorbital development, platycephaly, and occipital bunning. The pattern appears inverted as far as the Late Pleistocene representatives of *Homo sapiens* (together with KNM-ER 1813 and Irhoud 1) are concerned.

In terms of allometry, a shared size-related component of the shape is not expected, when the similar cranial capacity in Neandertals and modern humans are considered. Actually, the correlation between cranial capacity and the overall shape variation is not significant, although RW1 shows a certain relationship with encephalization (Figure 7). Considering a possible trajectory (variation in shape related to variation in size) from the small *Homo habilis* KNM-ER 1813, to the largest specimens, Neandertals are rather aligned with a generalized archaic allometric pattern, while modern humans apparently show a marked displacement from this pattern.

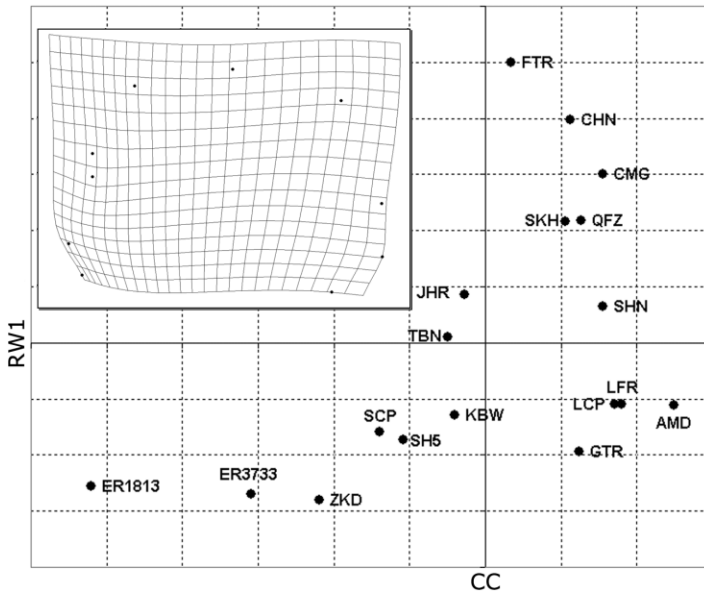


Fig. 7. Cranial capacity plotted onto RW1. The grid displays the deformation along the size axis (positive extreme).



Finally, a few notes may be added for the Italian specimens. It is remarkable that both the Eemian and the Würmian Neandertals from Italy – respectively represented by the Saccopastore and Guattari crania – are close to each other within the shape space (Figure 2, 5). In this light, both crania display a strong expression of the derived Neandertal traits, combined with high degree of platycephaly, even greater than in the other specimens of the same group. Does this suggest phenetic homogeneity among the Italian Neandertals (despite their different chronology, as well as the well known differences in size and discrete anatomy<sup>10</sup>)? We consider that their common morphometric pattern may be only noticed. It combines plesiomorphic retentions and clear apomorphic expression of traits (yet always at the extreme pole of the Neandertal range of variability). Moving into the modern pole, the early Neolithic cranium from Abruzzo (Fonterossi), close to the

position of the Magdalenian specimen from Chancelade, well represents the anatomically modern cranial shape – *i.e.*, rounded braincase and reduced, orthognathic face.

### Patterns in the evolution of the genus *Homo*

What follows is a discussion of the results reached in this work, with the cautionary premise that it was based upon a limited number of fossils (some among the most complete fossil human crania) and referred to a single bidimensional plane (although particularly significant). Therefore, we will simply suggest inferences upon the phenetic patterns observed, and avoid to evaluate the position of single specimens in human evolution (despite the general consistency of their distribution in our analyses). As a general reference, in Figure 8 the distribution of cranial shape values (shape vector computed by tpsPLS software) of the entire

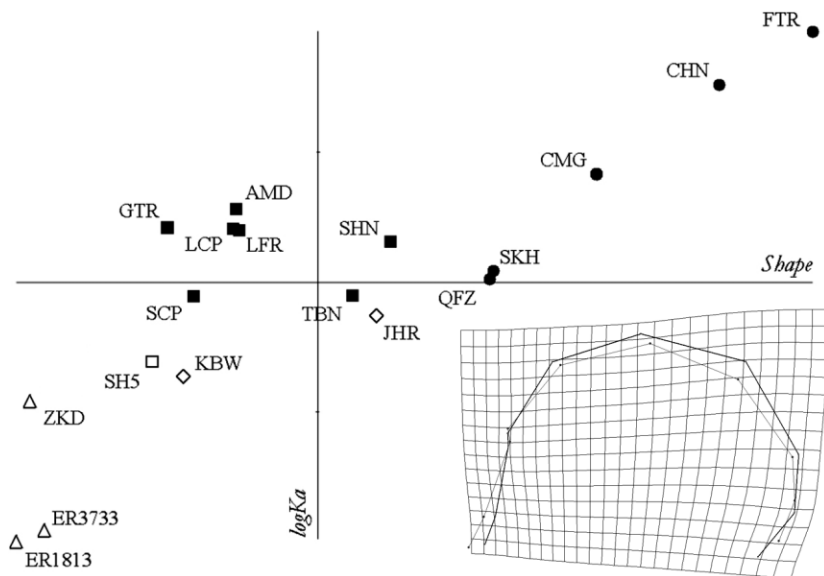


Fig. 8. Values along the shape vector (linear combination of shape scores) of each specimen are plotted against a time scale (log-Ka). The grid shows the warp of the configuration of landmarks from the Irhoud specimen toward Fonterossi (bold line).

sample (with the exception of Sts 5) are plotted against the chronological position of each specimen, expressed as approximate estimation in log-ka (logarithm of thousand years before present). Clearly, this is just a descriptive representation, and the logarithmic time scale is but a useful way to visualize a synthetic pattern of variation.

The two Early Pleistocene African specimens KNM-ER 1813 and KNM-ER 3733, taken together, may be considered as representative of an ancestral morphotype. Their midsagittal cranial profiles appear closely related between each other, despite arguments about their affinities and taxonomic positions, as *Homo habilis* or *Australopithecus habilis* and *Homo ergaster* or *Homo erectus* respectively<sup>9,15–17</sup>. From this point of view, both the specimens could possibly be referred to very close *taxa*, especially when the evidence furnished by the cranial sample from Dmanisi, Georgia, is considered<sup>18</sup>. Interestingly, elsewhere in our analysis (Figures 5, 7) KNM-ER 1813 shows an overall phenetic affinity with Sts 5, while the more derived KNM-ER 3733 appears close to the typical *Homo erectus* morphotype, represented here by the reconstruction based on specimens from Zhoukoudian.

More than one million years later, at about the boundary between Early and Middle Pleistocene or later, the ancestral African morphotype seems to have been involved in (at least) two evolutionary trajectories. One of them retains the same overall midsagittal cranial shape encountered in *Homo ergaster*, though increasing in size (this is the Asian, or typical, *Homo erectus*), while the other cranial shape moves toward a different morphological pattern, apparently shared among the Afro-European Middle Pleistocene hominids (possibly included in *Homo heidelbergensis*<sup>23</sup>). Human variability in this time range thus shows a mixture

of traits in cranial morphology and dimensions<sup>19</sup> that was probably due to that wide geographic and ecological distribution rapidly reached by our genus after its appearance<sup>20,21</sup>. Some independence from environmental constraints (implied by behaviorally and technologically based strategies) might have had an active role in such a diversification<sup>22</sup>. The phenetic continuity between specimens and samples that we observe among this variability may suggest a taxonomic ranking of the Middle Pleistocene specimens from Africa and Europe in a single, variable and widespread species, referred to as *Homo heidelbergensis*<sup>23</sup>, although differences between African and European populations (disregarding the Asian diversity still referable to *Homo erectus*, or the possible existence in that continent of more than one species) may be anyway acknowledged<sup>24</sup>.

Nevertheless – that is, independently from the number of species that are effectively represented in the fossil record of the Middle Pleistocene – two unambiguous evolutionary lineages in terms of cranial morphology are discernible later. One of them should be referred to the Neandertal morph, or *Homo neanderthalensis*, and the other moved – most probably in Africa – towards the emergence of modern humans, or *Homo sapiens*. The Neandertal lineage finds a progressive characterization throughout the Atapuerca Sima de los Huesos sample (represented here by the most complete specimen SH 5) and the early Neandertal from Saccopastore. The latter, in particular, retains a somewhat plesiomorphic architecture of the vault profile, while shows a derived design of the face, characterized by a pronounced midfacial prognathism. Subsequently, the Würmian Neandertals show a rather large degree of variation in a penecontemporaneous context and limited geographical range. Anyway, all the specimens share a peculiar midsagittal

profile of the cranium, that suggests an independent lineage, and a derived (yet archaic) morphotype.

The status of Near-Eastern Neandertals such as Amud, Shanidar 1, and Tabun is less clear. In the multivariate context of our analysis (see, e.g., Figures 5, 7, and 8), they show a general Neandertal pattern (particularly in the face), but Shanidar and Tabun appear displaced towards a more »modern« cranial shape. The systematic position of these fossils is not particularly debated<sup>31</sup> while, at the same time, the hypothesis of a close genetic link with early (i.e. »interglacial«) European Neandertals, such as those from Saccopastore, has been put forward. In view of the chronology and geographic distribution of these specimens, combined with their slightly pronounced Neandertal traits, the evolutionary dynamics of these Levantine populations is of special interest and should be further investigated.

The trajectory towards modern humans introduces an autapomorphic model in the development of the cranial vault, mainly characterized by frontal enlargement and exclusively derived parieto-occipital curvature, displaying a wide phenetic variability for a relatively short chronology (unexpected with respect to the similar range of variation displayed by the heterogeneous group of archaic humans, spanning for a much longer period of time). The specimens usually referred to *Homo sapiens* (or anatomically modern humans) are clearly separated from the other samples, and find in the still archaic specimens from Jebel Irhoud a possible precursor. This new architecture of the midsagittal cranial profile, clearly displayed in the Near-Eastern samples from Skhul and Qafzeh and in the typical Cro-Magnon cranium, is further developed in more recent humans as Chancelade and Fonterossi.

Also the midsagittal profile of the face (from *nasion* to *prosthion*) in modern humans suggests the occurrence of a structural model that is in contrast with the midfacial protrusion of the Neandertals.

Thus, according to other sources of information<sup>25–28</sup>, our analysis demonstrates that Neandertals and modern humans are distinct morphotypes and probably belong to independent evolutionary lineages. Another more detailed analysis carried out on the midsagittal profile of the cranial vault, only has previously suggested this morphological gap between *Homo neanderthalensis* and *Homo sapiens* representatives, and was interpreted as the occurrence of different evolutionary trajectories<sup>29</sup>. It appears therefore appropriate to refer to Neandertals and anatomically modern humans as different phylogenetic and taxonomic units (i.e. species), in spite of any possible inference on their reproductive status, including the possibility of some occasional interbreeding<sup>30</sup>.

Of special interest is the position of the Moroccan Irhoud 1 cranium, as far as morphology, chronology, and topology are also considered. It displays a progressive midsagittal profile, combining a modern-like structure of the face (plesiomorphic and relatively small) with a rather derived (not particularly platycephalic) vault shape. It seems therefore probable that this specimen belongs to the evolutionary trajectory of *Homo sapiens* – as indicated by various authors<sup>13,32</sup> – although not (yet) referable to the fully modern morphotype. The comparison between Irhoud 1 and the fully modern midsagittal profile of Fonterossi (warped in Figure 8), shows in the former specimen a rather derived face and frontal areas, but a flattened parietal outline.

In synthesis, regardless of the position of samples or single specimens in the scenario discussed in this paper, the variability of the genus *Homo* – as described

here by means of the displacement of landmarks along the midsagittal profile of the cranium (mandible excluded) – appears clearly polarized, with a first principal component of the multivariate analysis (see Figure 5) that explains 62% of the total variance, and approximates the significance of a discriminant function between modern and non-modern specimens. In this scenario, what we found remarkable is the occurrence of heterogeneous but generically archaic *taxa*, at one pole, and the modern range of variation that occupies alone the opposite pole. In the archaic variability, a relatively large but modern-looking facial morphology is associated with a primitive structure of the vault. A rather different pattern characterizes the Neandertal lineage (as observed also in the comparisons between single specimens), where a derived midfacial protrusion combines with an archaic braincase (Figure 4). By contrast, the evolutionary trajectory leading to modern humans is described by the maintenance of a plesiomorphic shape of the face (although reduced in relative dimensions), in association with a derived developmental pattern of the cranial vault. This distribution in the shape space of archaic and modern sub-samples apparently suggests two discrete entities with comparable ranks of morphological potentiality, or (better) similar evolutionary independence – the archaic and the modern, where in the former the vault shape changes and the reduction of the facial structures seem to be related to size (Figure 7). The development of cranial capacity – the process known as »encephalization« – involves some allometric responses within the archaic structural system of the human cranium that must be further considered. On the other side, modern humans apparently show a sharp departure from this allometric *continuum*.

Since this work was completed (summer 2001), a number of relevant papers

have been published and some of them must be briefly acknowledged here. The vault globularity has been proposed as a real »autapomorphic character« for *Homo sapiens*, by virtue of its structural interaction with facial reduction and changes in cranial base angle<sup>33</sup>. These relationships have been accurately described by means of geometric morphometrics by Lieberman and co-workers. The morphological gap between modern humans and other *taxa* of the genus *Homo*, for the vault profile described in earliest analyses<sup>29</sup>, has been therefore widely confirmed. Considering the influence of the brain development, the temporal lobes have been hypothesized to have a major role in the structural cranial module of modern humans. In contrast, according to this paper and to some recent endocranial analyses<sup>34</sup>, the parietal areas should be carefully considered. Following the same approach, further information has been developed on the structural correlation between vault and face, including the relationships with ontogeny and cranial base development<sup>35</sup>. Some caution has been recommended when inference on phylogeny are developed on these functional bases, but the structural interdependence between face and vault has been remarked and tested carefully. It has been also claimed that Neandertals do not display a midfacial prognathism, but that (conversely) modern humans just evolved a reduction of the facial skeleton<sup>36</sup>. According to our data, KNM-ER 3733 shows a certain degree of midfacial growth, considering its value along the PC2. In contrast, the pairwise comparisons failed to suggest a clear midfacial protrusion. Thus, our analysis does not confirm at present this hypothesis. However, a larger sample size would be necessary to test whether or not the Neandertal midfacial prognathism represents a scaled expression of an ancestral morphotype.

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*pologicum*. Our work published here was developed in the framework of the first years of such a collaborative experience. A number of people contributed with suggestions and encouragement, including the accurate and helpful review ultimately accomplished by the anonymous referee of this journal – we are sincerely grateful to all of them.

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## **VARIJACIJE OBLIKA LUBANJE U RODU *HOMO* – GEOMETRIJSKO-MORFOMETRIJSKI PRISTUP**

### **S A Ž E T A K**

Mediosagitalni profili lubanja različitih taksona roda *Homo* su analizirani geometrijsko-morfometrijskim tehnikama. Usporedba jednog uzorka korištenjem thin-plate-spline funkcije pokazuje srodnu komponentu, koja opisuje trend zastupljen u cijeloj ljudskoj liniji s afinom komponentom (povišenje zatvorenog dijela lubanje i zaravnjenje lica). Istovremeno, ne-afina komponenta pokazuje uzorak distorzije koji se pojavljuje na licima Neandertalske linije (prognatizam srednjeg dijela lica) i drugi koji se pojavljuje na zatvorenom dijelu lubanje modernih ljudi (fronto-parijetalno povećanje). Osnovna komponenta analize pokazuje »bimodalnu« varijabilnost, koja opisuje prvi arhaični stup, uglavnom heterogen u taksonomskom smislu, te moderni. Prve dvije osnovne komponente (koje objašnjavaju 80% varijance) uključuju fronto-parijetalnu ekspanziju i prognatizam središnjeg dijela lica. Ove karakteristike stavljaju Neandertalsku liniju i modernu liniju na zasebne trajektorije, i dopuštaju identifikaciju diskretnih elemenata u generalnoj pojavi ljudske evolucije.