

Landmark-Based Shape Analysis of the Archaic *Homo Calvarium* from Ceprano (Italy)

Emiliano Bruner and Giorgio Manzi*

Dipartimento di Biologia Animale e dell'Uomo, Università "La Sapienza", Rome, Italy

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ABSTRACT The Ceprano calvarium represents one of the most important sources of information about both the dynamics of the earliest hominid dispersal toward Europe and the evolution of the genus *Homo* in the early-to-middle Pleistocene. In this paper, the midsagittal vault profile and the 3D frontal bone morphology of Ceprano are investigated comparatively, using landmark coordinates and Procrustes superimposition. In fact, despite the fact that the skull appears partially distorted by diagenetic pressures (thus precluding a comprehensive landmark-based analysis), some aspects of the overall morphology are suitable for consideration in terms of geometric morphometrics. The midsagittal profile shows an archaic shape, comparable with the *H. ergaster/erectus* range of variation because of the fronto-parietal flattening, the development of the supraorbital and nuchal structures, and the occurrence of a slightly larger occipital bone. By con-

trast, the frontal bone displays a derived 3D shape that, mostly because of the widening of the frontal squama, appears comparable with the Afro-European variation of the Middle Pleistocene (i.e., *H. heidelbergensis/rhodesiensis*). Taking into account the unique morphological pattern displayed by Ceprano, its role as a link between early *Homo* and the Middle Pleistocene populations of Europe and Africa is not falsified. Thus, when aspects of the Ceprano's morphology are described within the analytical framework provided by geometric morphometrics, the relationships between Ceprano and the subsequent Afro-European fossil record are emphasized, suggesting the occurrence of an ancestral stock of *H. heidelbergensis/rhodesiensis* that is properly represented by the Italian specimen. *Am J Phys Anthropol* 132:355–366, 2007.

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Fragments of a heavily fossilized human cranium were discovered in 1994 in the countryside between the towns of Ceprano and Pofi in southern Lazio, about 100 km from Roma (Italy). The clay layer where they were found was stratigraphically attributed to more than 700 ka, and the human fossil itself has been dated to a probable time-range spanning between 800 and 900 ka (Ascenzi et al., 1996, 2000; Ascenzi and Segre, 1997a,b; 2000; for a review, see Manzi, 2004a).

The cranial fragments were submitted to a challenging process of restoration, which started just after the discovery and was completed in 1999, with the result of reassembling a rather complete human calvarium, internationally referred to as "Ceprano" (see Fig. 1). It is based on the original reconstruction by Ascenzi et al. (1996), which was subsequently corrected by Clarke (Ascenzi and Segre, 2000; Clarke, 2000), and further revised by de Lumley and Mallegni, with their respective coworkers (Ascenzi et al., 2000). The reconstruction is composed by the virtually complete frontal bone, the frontal processes of both the zygomatic bones, part of the sphenoid, the largely preserved right parietal and occipital bones, important portions of both of the temporals and fragments of the left parietal. The main difference between the first and the final reconstruction concerns the relationship between the anterior and posterior regions. This relationship now rests on the articulation between the frontal and the right parietal, along two segments of the coronal suture and with the greater wing of the sphenoid, which also articulates with the temporal squama on the endocranial surface of the same side. On the left, the temporal bone is connected with the preserved part of the sphenoid, which in turn articulates with the frontal. Thus, the fundamental result

obtained with the final reconstruction is that each bone connects with others appropriately, while some connections were previously represented by areas covered by gypsum. As a consequence, the cranium is slightly shorter than before and the shape of the cranium displays a more uniform outline in lateral view, because the anterior and posterior districts have been inversely rotated to articulate with each other.

It should be observed that, in posterior view, the Ceprano calvarium appears affected by some deformation, since the better preserved right parietal appears unnaturally angulated at the level of the temporal lines, with a rather vertical lateral wall, in contrast with the heterolateral parietal profile, which appears more oblique. It has been suggested (Manzi, 2004a) that this asymmetrical pattern is due, at least in part, to diagenetic pressures acting downward and heterolaterally upon the left parietal (which is also, and consequently, largely missing). Therefore, the vault appears slightly

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*Correspondence to: Giorgio Manzi, Università di Roma "La Sapienza", Dipartimento di Biologia Animale e dell'Uomo, 00185 Roma, Italy. E-mail: giorgio.manzi@uniroma1.it

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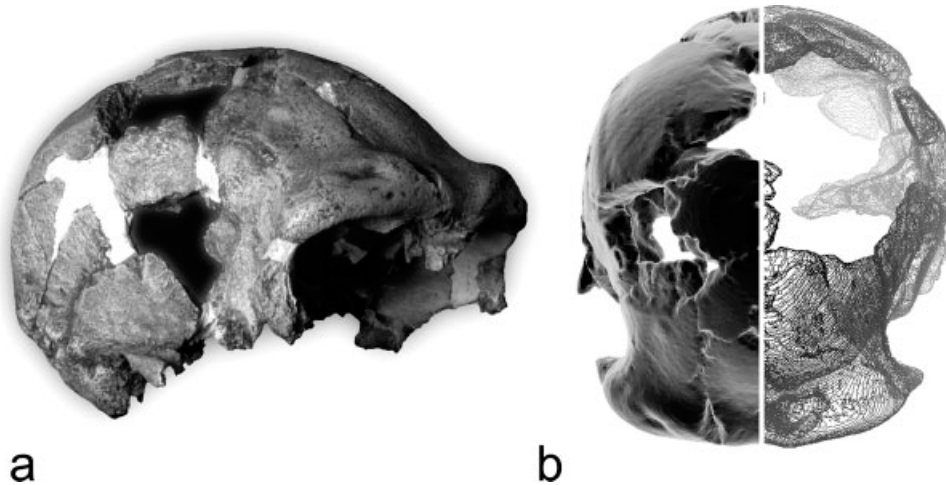


Fig. 1. The Ceprano calvarium (a) and its digital reconstruction in dorsal view (b) after computed tomographic analysis through 3D rendering (right side) and polylines interpolation (left side). See Bruner and Manzi, 2005 for further details.

compressed on the left and bent on the right, because of the comparable but opposite deformations of the two sides. A recent exploratory attempt to evaluate this deformation was carried out and briefly discussed elsewhere (Bruner and Manzi, 2005), where it has been shown that an averaged shape of the cranial vault (as a consensus profile between the left and the right sides, controlled through landmark-based techniques) exhibits a low-positioned maximum breadth, with nonparallel and convergent parietal walls. In this light, we may make the following assumptions: a) the absolute value of the main cranial breadth should not be involved, since the coronal surface of the cranium was simply shifted towards the right side; b) the cranial height might be only slightly reduced, as a consequence of the downward vault flattening on the left side; c) it seems that both the frontal and the occipital are not significantly affected by this process.

The specimen has already been evaluated in some detail and compared to the pertinent fossil record by means of different heuristic approaches (Ascenzi et al., 1996, 2000; Clarke, 2000; Manzi et al., 2001; Mallegni et al., 2003; Bruner and Manzi, 2005). At present, despite the taxonomic position of Ceprano remains controversial, a consensus has been reached regarding the phylogenetic significance of this calvarium. In fact, its morphological pattern is considered to be similar, but distinguishable, from those of *H. ergaster* and *H. erectus*, showing some affinities with later *Homo* morphs, i.e., those currently referred to *H. heidelbergensis*. In this light, “Ceprano can be considered as a good candidate to represent the last common ancestor for this latter group of hominines, ultimately between Neanderthals and modern humans” (Manzi et al., 2001). Nevertheless, from a taxonomic point of view, it has been alternatively referred to a “late” variant of *H. erectus* (Ascenzi et al., 1996), to *H. erectus sensu lato* (Clarke, 2000), to a possible adult representative of *H. antecessor* (Manzi et al., 2001; Manzi, 2004a,b; Bruner and Manzi, 2005), or even to the new species *H. cepranensis* (Mallegni et al., 2003).

The present paper is aimed at quantifying the morphological affinities and differences between Ceprano and other archaic human morphs, using landmark-based tools. Thus, focusing on the cranial shape, the morphology of the last reconstruction of the Ceprano calvarium is comparatively examined using geometric coordinates, Procrustes superimposition, and thin-plate spline (see

Rohlf and Marcus, 1993; Adams et al., 2004; Zelditch et al., 2004). The final goal is not necessarily a taxonomic or a phylogenetic assessment of the Italian specimen, but rather the analytical (i.e., quantitative) evaluation of those similarities and differences that may be broached even in terms of a general description. Paleoanthropology in fact relies upon sample sizes that rarely allow a full statistical approach to the morphological differences, underexpressed within-group variations, and fragmented specimens reconstructed according to the personal experience of the anatomists. Therefore, these kinds of analyses must be regarded as explorative and descriptive. Nevertheless, the geometric-morphometric approach allows to go far beyond the mere description of differences, providing tools that quantify the available variation and order the information according to conventional algebraic procedures. The superimposition techniques offer a shared background on how to compare the shape variation, and the theory of shape provides a common analytical framework within which morphologists can discuss their results (Zelditch et al., 2004). Therefore, such information is propaedeutic to provide, support, or falsify, any hypothesis that may come out from the evaluation of the fossil evidence.

MATERIALS AND METHODS

In view of the deformation of the braincase due to diagenetic pressures, the analysis was restricted to features supposed to be truly informative with respect to the shape of the cranium, namely the midsagittal profile and the overall shape of the frontal bone.

Despite some missing parts, the midsagittal profile of the cranial vault is apparently well defined in Ceprano, since the distortion of the skull deformed the lateral (i.e., parasagittal) structures more than the midsagittal contour. Furthermore, it is well known that the profile of the cranial vault in lateral view is a reliable source of information in terms of evolutionary and structural items, especially in a comparative context (Lieberman et al., 2002). In turn, also the frontal bone of Ceprano does not seem affected by the diagenetic distortion, showing only minor asymmetries in both the ecto- and endocranial structures. At the same time, the frontal bone has already been demonstrated to be particularly useful in characterizing this specimen (Ascenzi et al., 1996; Manzi

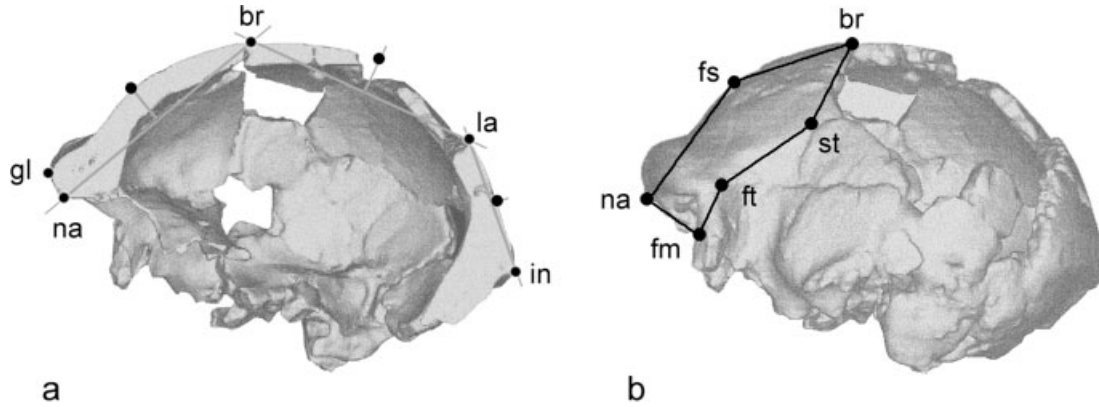


Fig. 2. Configurations. (a) midsagittal vault profile (na, nasion; gl, glabella; br, bregma; la, lambda; in, inion); points between homologous landmarks were localized on the vault outline through orthogonal projection at the 50% of the chord between the respective landmarks. Note that in Ceprano the parietal projection is extrapolated from the available surface. (b) frontal bone (na, nasion; fm, frontomolare orbitale; ft, frontotemporale; br, bregma; st, stephanion; fs, frontal squama, at the 50% of the outline nasion-bregma).

et al., 2001; Mallegni et al., 2003; Bruner and Manzi, 2005).

The midsagittal profile of the reconstructed calvarium from Ceprano (Ascenzi et al., 2000) was analyzed through 2D-coordinates using a configuration of eight landmarks (Fig. 2a). This configuration includes three homologous (nasion, bregma, lambda), two structural (glabella, inion), and three constructed landmarks. The latter represent the projection on the esocranial outline of the midpoint from the chords nasion-bregma, bregma-lambda, and lambda-inion respectively. These types of points are semilandmarks because of their dependence from other structures and reduced degree of freedom. Semilandmarks can be used tentatively as full landmarks, weighted according to the decreased amount of information provided, or slid along tangent projections according to closer points (Zelditch et al., 2004). In our case, the homologous landmarks are too few to allow to rely upon tangent sliding. Therefore, also in view of the phenetic aim of this paper, the first approach was used and semilandmarks were considered as full landmarks.

Comparative data was taken from perigraphies reported in the literature and corroborated with direct sampling on casts (for more information on both sample and configuration, see: Manzi et al., 2000; Bruner et al., 2004). Unfortunately, some perigraphies lacked a proper scale and it was not possible to compute the centroid size (the square root of the summed square distances of each landmark from the centroid of the configuration). Coordinates were sampled using tpsDig 1.2 (Rohlf, 1998a). The sample ($N = 22$) includes different *taxa*, all attributed to the genus *Homo* (Table 1).

Because of the incompleteness of the Ceprano calvarium, its midparietal landmark point (orthogonal projection of the intermediate point along the bregma-lambda chord) was estimated. This estimation was not performed using a missing value recomputation of the available data from the comparative sample. The uncertainty of Ceprano's taxonomic position and its peculiar morphology make this approach rather unsatisfactory. We therefore considered more appropriate and informative to interpolate the profile visually by following the preserved portions of the outline, mainly in relation to its anterior component. Of course, this approach is more subjective than a statistical averaging and recomputa-

tion, since the result is conditioned by the personal experience and skillfulness of the anatomists that worked on the reconstruction.

The 3D shape of the frontal bone was analyzed using a nine landmark bilateral configuration, including nasion, frontomolare orbitale, frontotemporale, bregma, stephanion, and a semilandmark at the 50% of the curve nasion-bregma (Fig. 2b). Coordinates were sampled using a Microscribe 3DX. Comparative data was collected on first-quality casts ($N = 27$) preserved at the Museum of Anthropology of the University "La Sapienza" (Roma). A structural separation between squama and torus was recently described in Ceprano (Bruner and Manzi, 2005), and interpreted as a plesiomorphy shared with *H. ergaster/erectus* and not with the specimens from the Middle Pleistocene in Africa and Europe. Therefore, glabella and supraglabellar landmark points were not included in the present configuration to avoid a characterization which would be largely based on this known feature. In the 3D analysis of the frontal bone the centroid size was used as size index.

Following the geometric morphometric approach, the landmark systems representing each specimen are superimposed and normalized to minimize the differences in the position of the corresponding landmarks (Bookstein, 1991). According to the Procrustes registration, the configurations are translated to a common centroid, scaled to unitary centroid size, and rotated in order to minimize the least-square differences between corresponding landmarks (see also Rohlf and Slice, 1990). The residuals after the Procrustes superimposition are used to perform multivariate ordination analyses, after a proper reduction of the shape variables to match the correct number of degrees of freedom (see Zelditch et al., 2004 for further details). The coefficients from the resulting vectors are used to visualize the displacements of the landmarks along the multivariate axes. Landmark-based morphometrics thus allow to describe the actual covariation between structures, analyzing the position of each landmark relatively to the given configuration of landmarks. Such approach is more powerful than the analysis of single diameters (like in the traditional morphometric approach), than are useful to quantify metric variations and shape components, but cannot provide information on the geometry and

TABLE 1. List of the specimens, their taxonomic attribution, and inclusion in the analyses

Specimen	Label	Taxon	2D	3D
KNM-ER 1813	ER1813	<i>H. habilis</i>		*
KNM-ER 3733	ER3733	<i>H. ergaster</i>	*	*
KNM-ER 3883	ER3833	<i>H. ergaster</i>		*
Dmanisi 2280	DM2280	<i>H. habilis/ergaster</i>		*
Zhoukoudien III	ZKD3	<i>H. erectus</i>		*
Zhoudoudien XI	ZKD11	<i>H. erectus</i>	*	*
Ngandong XII	NGD12	<i>H. erectus</i>		*
Sambungmacan3	SMB3	<i>H. erectus</i>		*
Bodo	BOD	<i>H. heidelbergensis</i>		*
Kabwe	KAB	<i>H. heidelbergensis</i>	*	*
Petralona	PTR	<i>H. heidelbergensis</i>		*
Atapuerca 5	ATA5	<i>H. heidelbergensis</i>	*	
Tabun 1	TAB	<i>H. neanderthalensis</i>	*	*
Shanidar	SHA	<i>H. neanderthalensis</i>	*	
Amud	AMD	<i>H. neanderthalensis</i>	*	
Saccopastore 1	SCP1	<i>H. neanderthalensis</i>	*	
La Quina 5	LQN	<i>H. neanderthalensis</i>		*
La Ferrassie	FRS	<i>H. neanderthalensis</i>	*	*
La Chapelle-aux-Saints	CHP	<i>H. neanderthalensis</i>	*	*
Guattari	GTT	<i>H. neanderthalensis</i>	*	
Djebel Ihroud 1	IHR	<i>H. helmei?</i>	*	*
Qafzeh 9	QFZ9	<i>H. sapiens</i>	*	*
Skhul 5	SKH5	<i>H. sapiens</i>	*	*
Cro-Magnon 1	CRO	<i>H. sapiens</i>	*	*
Cro-Magnon 2	CRO2	<i>H. sapiens</i>		*
Vestonice 3	VST3	<i>H. sapiens</i>		*
Oberkassel	OBE	<i>H. sapiens</i>		*
Predmost 3	PRD3	<i>H. sapiens</i>		*
Predmost 4	PRD4	<i>H. sapiens</i>		*
Combe Capelle	CCP	<i>H. sapiens</i>	*	*
Chancelade	CHA	<i>H. sapiens</i>	*	*
Grotte des Enfants	GDE	<i>H. sapiens</i>	*	
Australian native	ABO	<i>H. sapiens</i>	*	
Maiella	MAI	<i>H. sapiens</i>	*	
Recent Ainu	AIN	<i>H. sapiens</i>	*	
Ceprano	CPR	<i>H. antecessor?</i>	*	*

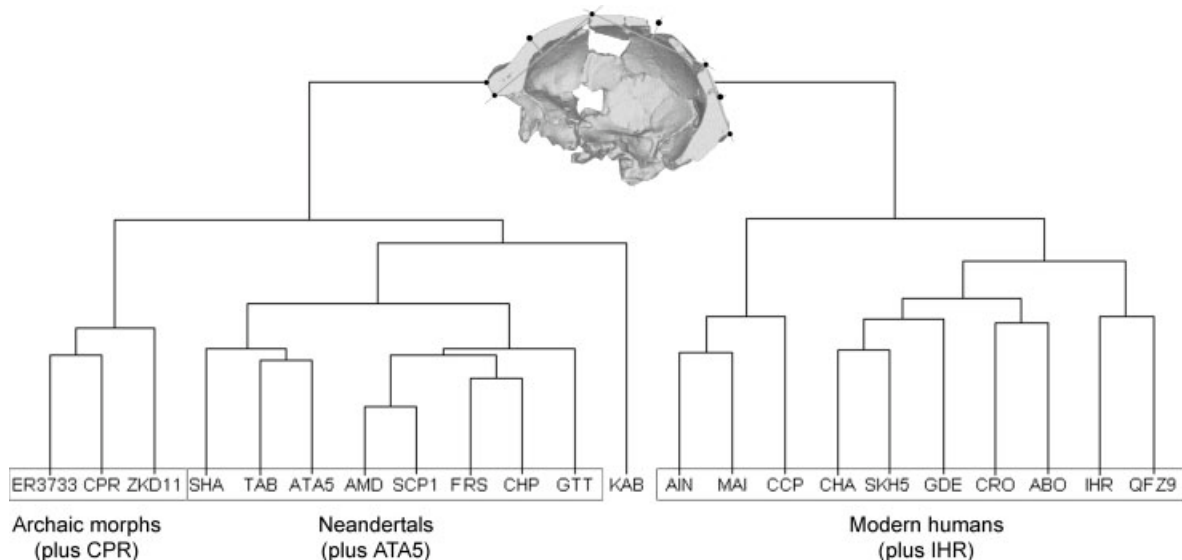


Fig. 3. The phenogram shows the morphological affinity for the midsagittal profile between specimens according to Procrustes distance and UPGMA (cophenetic correlation coefficient = 0.81). See Table 1 for labels.

actual spatial relationships of the anatomical structures (Rohlf and Marcus, 1993).

Phenetic affinities within the samples were analyzed through Procrustes distances and the unweighted pair-group method using an arithmetic averages procedure

(UPGMA). The distance matrix was computed using tpsSmall 1.19 (Rohlf, 1998b) and the clustering procedure performed through SynTax (Podani, 2000). A principal component analysis was carried out using tpsRelw 1.18 (Rohlf, 1998c) and Morphologika (O’Higgins and

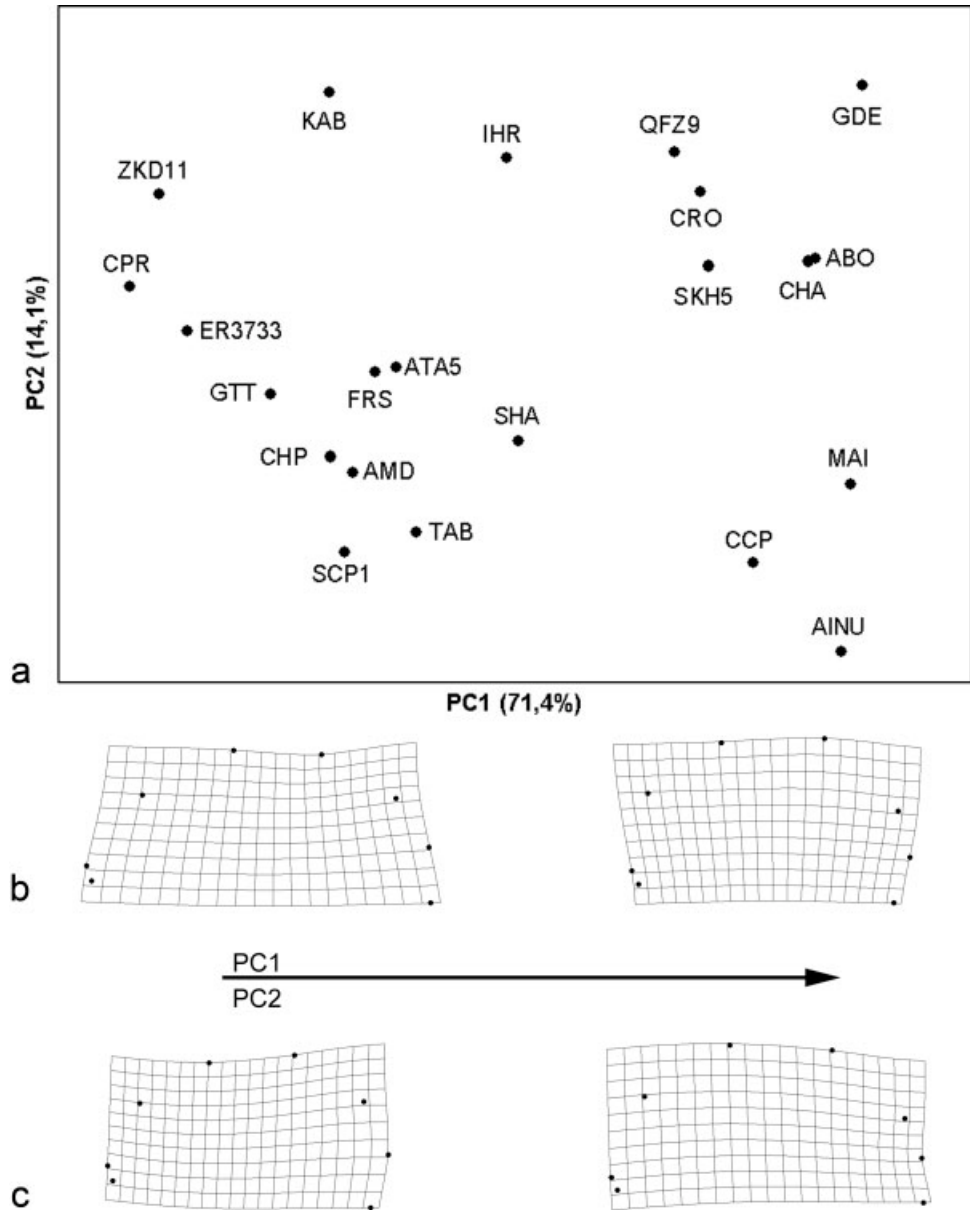


Fig. 4. (a) Principal component analysis of the midsagittal profile. The first two components explain 86.9% of the total variance. PC1 is mostly associated with a relative development of the fronto-parietal areas (b); PC2 is characterized by the reduction of the occipital bone (c). See Table 1 for labels.

Jones, 2004). Centroid size was calculated using APS 2.3 (Penin, 2000). Pairwise comparisons were visualized using Morpheus et al. (Slice, 2000). Bending energy was calculated using tpsSpline 1.15 (Rohlf, 1997).

RESULTS

Midsagittal vault profile

According to the cluster procedure computed on the midsagittal vault profile, the genus *Homo* displays the distinction between two main patterns, respectively referred to the modern vs. the non-modern ranges of variation (Fig. 3; cophenetic correlation coefficient = 0.81). Within the non-modern variability, the main cluster groups both the West and East Neandertals, the “early” Neandertal Saccopastore 1, and Sima de Los Huesos cranium 5. The African Middle Pleistocene cranium Kabwe 1 stands alone outside this main group. The second and smaller cluster is represented by the less derived

morphs, namely the *Homo ergaster/erectus* representatives and Ceprano. The modern cluster includes the late Middle Pleistocene specimen Ihoud 1 from North Africa.

The first principal component (71.4% of the shape variance; Fig. 4) separates the modern from the non-modern specimens. According to the small fraction of variance explained by the second and higher components, the morphospace is strongly polarized by this first axis of variation. Moving from the non-modern toward the modern pole, this component describes the enlargement of the upper (mostly parietal) areas and the consequent bulging of the entire profile, including vertical stretching and antero-posterior relative shortening of the frontal and occipital bones. The second component (14.1%) separates the modern variability into two groups; at the same time, it separates Kabwe and Ihoud from the other non-modern specimens. It is worth noting that Ihoud lies rather midway between Kabwe and the anatomically modern humans. Introducing the profile of a male *Pan troglodytes* as phenetic outgroup (data not shown) does not change

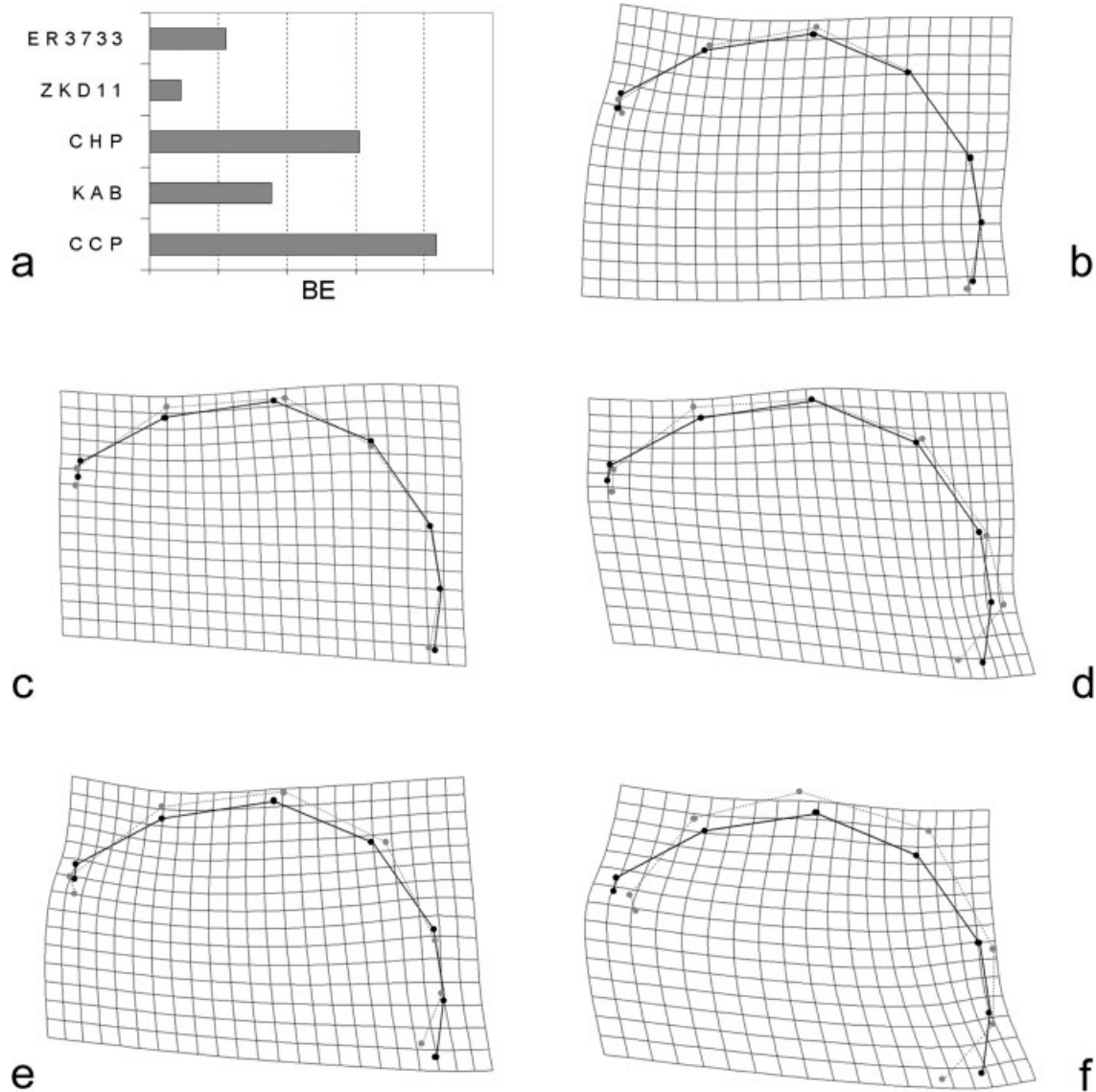


Fig. 5. The Ceprano neurocranial midsagittal profile is compared with some representative specimens, showing the bending energy values of the pairwise comparisons (a) and the thin-plate spline distortion grids after Procrustes superimposition from each specimen (thinner links) to the Ceprano configuration (thicker links): KNM-ER3733 (b), Zhoukoudian 11 (c), La Chapelle-aux-Saints (d), Kabwe (e), and Combe Capelle (f).

the cluster result but for the position of Ithoud 1, which clusters with Kabwe. This second component mainly involves a strong reduction of the occipital area and the relative vertical stretching of the frontal bone (see Fig. 4). Neandertals are characterized at the opposite end of this axis, because of their occipital development and relative frontal flattening. Excluding Kabwe and Ithoud, the non-modern sample shows a variance that is 2.8 times the variance expressed by the modern group on the first axis, while the modern shows a variance that is 3.4 times the non-modern one on the second component. Considering the two axes together, the sum of variances is comparable (modern/non-modern = 1.2).

The Centroid size cannot be computed for the 2D midsagittal analysis because of the lack of scale information on some specimens. Nevertheless, considering the comparable cranial capacity in modern humans and Neandertals (1496 ± 111 cc. and 1427 ± 150 cc. respectively;

Holloway et al., 2004) we can assume that these two components would not be influenced by shared allometric constraints.

Within this shape space (85.5% of the total variance), Ceprano is positioned close to the archaic representatives of the genus *Homo*, with a midsagittal vault profile characterized by a low frontal and parietal outline, associated with robust supraorbital and nuchal structures, and a backward projection of the occipital bone. It appears somehow intermediate between KNM-ER 3733 and Zhoukoudian 11, clearly differentiated from the patterns displayed by both the *H. heidelbergensis-neanderthalensis* variation, on one side, and from the African Middle Pleistocene crania (Kabwe and Ithoud), on the other.

Figure 5 shows the pairwise comparisons between the midsagittal vault profile of Ceprano and KNM-ER3733, Zhoukoudian 11, La Chapelle-aux-Saints, Kabwe, and Combe Capelle. Minor differences may be noted in speci-

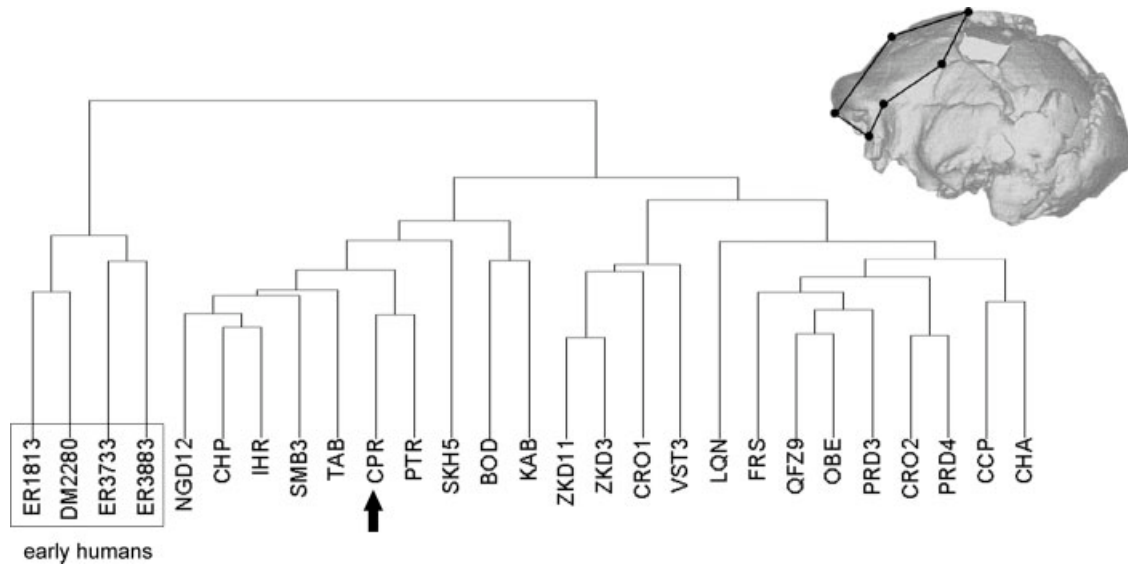


Fig. 6. The phenogram shows the morphological affinity for the frontal bone shape between specimens according to Procrustes distance and UPGMA (cophenetic correlation coefficient = 0.76). See Table 1 for labels 3.

mens referred to *H. ergaster/erectus*. These differences are associated with a moderate and relative fronto-parietal flattening in Ceprano. Compared with a classic Würmian specimen (La Chapelle-aux-Saints, that according to the PCA may be used as representative of the Neandertal cluster), Ceprano shows a light relative flattening of the frontal and parietal contour, with major differences related to a proportional reduction of the nugal structures in the Neandertal configuration. The development of the occipital superstructures is also visible in the comparison with Kabwe, associated with a generalized elevation of the vault, including the occipital upper scale in the latter (Fig. 5d). The same pattern is observed in comparing Ceprano with a modern human (i.e., Combe Capelle, which is the less different from Ceprano along the PC2), although it is evidently magnified. To quantify the differences between these configurations, the bending energy values of the thin-plate spline deformation grids may be used. It is worth noting that the Ceprano/Zhoukoudian 11 spline shows the lowest deformation, followed by that with KNW-ER 3733 (2.5 times the Ceprano/Zhoukoudian value), Kabwe (4.0), La Chapelle-aux-Saints (6.8), and Combe Capelle (9.3).

Frontal bone

The cluster procedure performed on the 3D coordinates taken on the frontal bone shows two main basic morphologies (Fig. 6 – cophenetic correlation coefficient = 0.76). The first group includes only specimens of early *Homo* from Africa and the Near East (*H. habilis*, *H. ergaster*, and Dmanisi 2280), while the second group includes all the other configurations. Although modern humans tend to display a certain similarity, no clear subgroups can be recognized within this second cluster, as far as chronology, phylogeny, or geography are concerned. Ceprano is included within this heterogeneous range of variation, showing the largest phenotypic affinity with Petralona.

In the shape space connected with the present frontal bone configuration (see Fig. 7), the first principal component (45.3% of shape variation) separates the skulls

from East Rudolf and Dmanisi from the rest of the sample, because of a vertical development of the frontal squama and the relative widening of its upper areas. This component reveals a certain correlation with the centroid size ($R = 0.59$; $P = 0.001$). Nevertheless, the bivariate comparison in Figure 8 shows that this correlation is rather spurious, since it is due to the consistent differences in both size and shape between early *Homo* and the other specimens. No allometric component can be described within the more derived *Homo taxa*.

The second component of the shape space (29.2%) enlarges the variation within the rest of the sample, describing the antero-posterior shortening of the frontal bone (mostly at the temporal fossa) and the relative widening of the whole shape. The configuration also undergoes a relative vertical compression at the temporal fossa, probably because of an absolute vertical stretching of the squama. The relative lengthening of the upper half of the bone suggests a more robust supraorbital torus. Ceprano (together with Kabwe, Bodo, Petralona, and La Chapelle-aux-Saints) is found at the positive extreme of this pattern.

In Figure 9, differences between Ceprano and other *taxa* are visible through pairwise comparisons after a Procrustes superimposition of the Ceprano configuration with the average shapes of early *Homo*, Asian *H. erectus*, and *H. heidelbergensis/rhodesiensis*. Compared to the early *Homo* configuration, Ceprano's frontal bone is taller and wider mostly because of the marked widening at the bistephanic breadth. The configuration of the Asian *H. erectus* specimens is more comparable with the Italian fossil, although it is more stretched antero-posteriorly. The *H. heidelbergensis/rhodesiensis* configuration shows an almost complete superimposition with the Ceprano shape, leaving only minor residuals.

DISCUSSION

As far as cranial morphology is concerned, the archaic human calvarium from Ceprano still represents the best preserved fossil evidence of the earliest European populations archaeologically known in this continent well

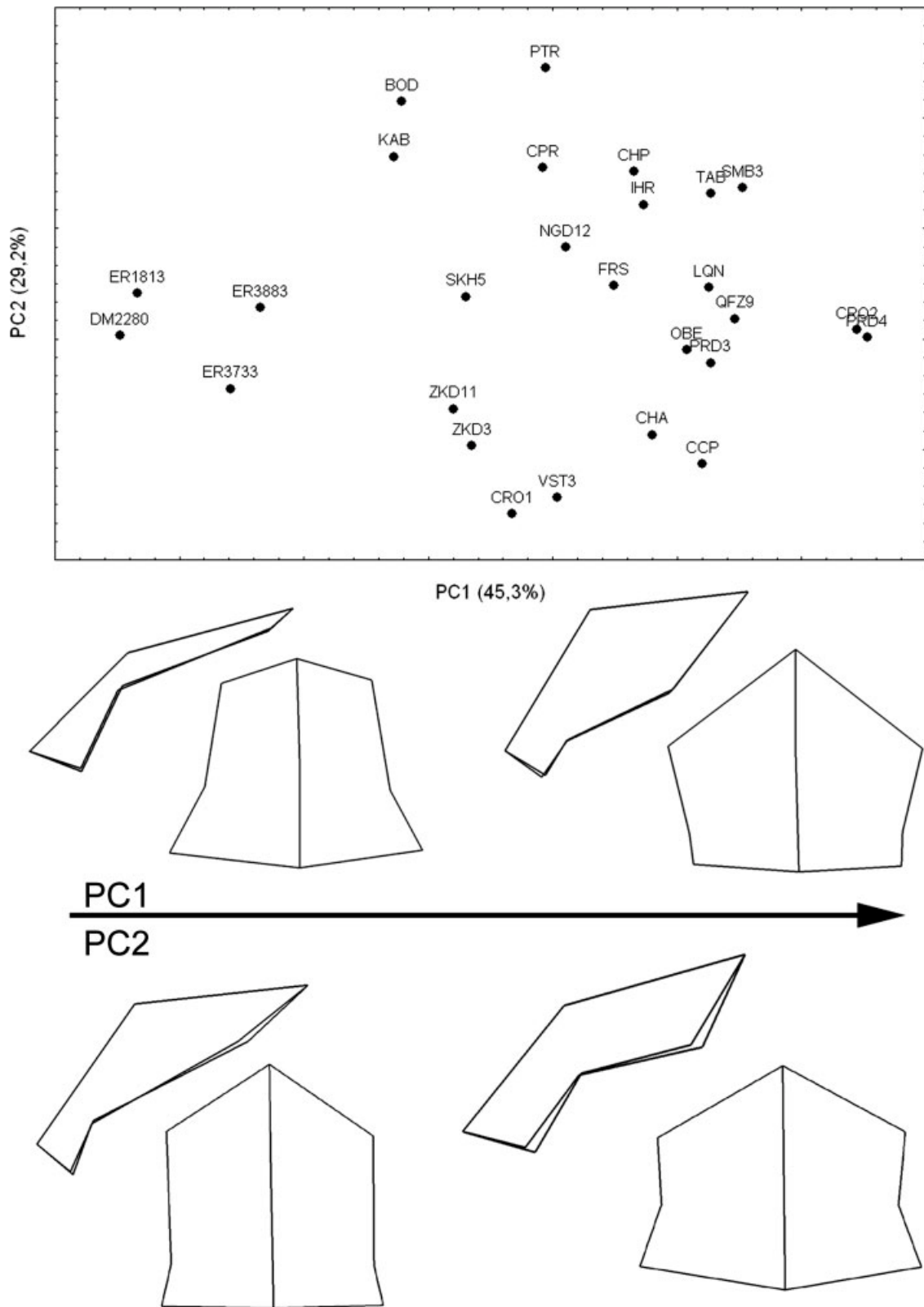


Fig. 7. Principal component analysis of the frontal bone shape. The first two components explain 74.5% of the total variance. The wire-frames (in left lateral and frontal view) show the pattern along these two axes, at the minimum and maximum values of the range. See Table 1 for labels.

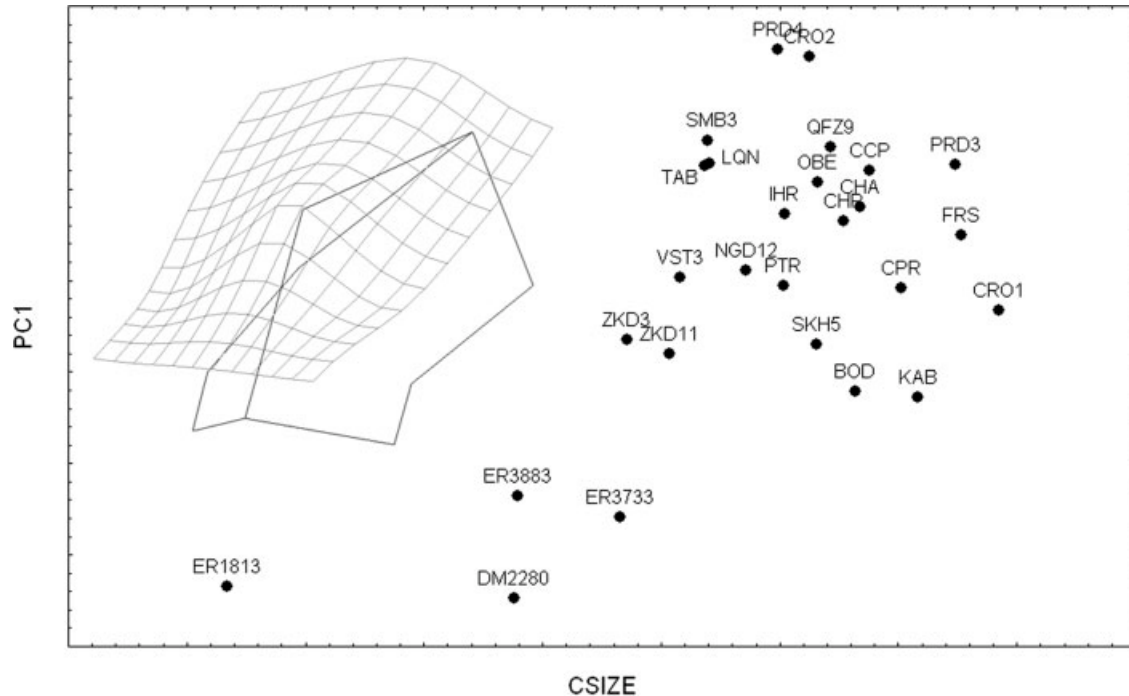


Fig. 8. Centroid size plotted onto PC1. The correlation between the two axes ($R = 0.59$; $P = 0.001$) is due to the differences in both size and shape between early *Homo* and the rest of the sample. The correlation within the latter subgroup is not statistically significant. The distortion grid shows the pattern along the first shape component from a skewed leftward perspective, showing the bulging of the frontal squama and the relative widening of the upper areas. See Table 1 for labels.

before the beginning of the Middle Pleistocene (Pares et al., 2006). By contrast, the coeval remains from Atapuerca-Gran Dolina (Arsuaga et al., 1999) are too fragmentary and belong to juvenile individuals whose phylogenetic and ontogenetic components are not readily distinguishable. Therefore, the morphology of the Ceprano calvarium appears crucial in the assessment of the relationship between the earliest Europeans, the African fossil record with comparable chronology (Abbate et al., 1998; Asfaw et al., 2002; Potts et al., 2004), and the various hypothetical *taxa* that are presently recognized across the Matuyama-Brunhes boundary (Manzi, 2004a).

Within this context, Ceprano exhibits a peculiar phenetic pattern, in which a plesiomorph general shape and some plesiomorph discrete traits are combined with more derived features (Ascenzi et al., 1996, 2000; Clarke, 2000; Manzi et al., 2001; Mallegni et al., 2003; Bruner and Manzi, 2005). Shape variations in cranial vault morphology provide important phylogenetic inferences about the evolution of the genus *Homo* and have already been investigated with geometric morphometric techniques (Manzi et al., 2000; Lieberman, 2002; Bookstein et al., 2003; Bruner et al., 2004; Harvati et al., 2004). In the light of these and other, more traditional, morphometric approaches (Stringer and Trinkaus, 1981), it is now well known that the ectocranial vault shape mostly discriminates between non-modern and modern humans, where the former group ranges from more archaic shapes to more encephalized and derived ones. From this perspective, the midsagittal profile of Ceprano may be regarded as unquestionably archaic, as already suggested by its platycephalic appearance and by the anatomical correspondence between inion and opistocranium. The calvarium displays a vault profile, which is comparable with those of the *H. ergaster/erectus* representa-

tives, because of the prominence of a massive supraorbital torus, the flattening of the vault, and the backward projection of the nuchal ridges.

According to our results, the frontal profile of Ceprano is also characterized by the relative independence between torus and squama, where a supratatorial sulcus separates the browridge from the anterior segment of the vault outline (Bruner and Manzi, 2005). This morphology is comparable with the *H. ergaster/erectus* hypodigm and different from that of the African Middle Pleistocene specimens. When the structural role of these regions in the neurocranium/splanchnocranium balance is considered (Lieberman, 2000), a different relationship between vault and face in these more archaic morphs in comparison to the subsequent Afro-European morphotypes of the Middle Pleistocene may be hypothesized. In particular, the reciprocal orientation of the braincase and the orbital area should be investigated further (Hylander et al., 1991). It is worth mentioning that the African specimens of the Middle Pleistocene included in the analysis occupy different positions. While the midsagittal profile of Kabwe clusters with the non-modern variation, that of Ihroud appears more derived, depending upon whether or not its facial shape or phenetic outgroup is included in the analysis. This is particularly interesting with respect to both the interpretation of the former African specimen as an advanced human morph (Rightmire, 2001) and the possible evolutionary relationship of the latter with the earliest anatomically modern humans in south-eastern Africa and Near East (Hublin, 2002; Stringer, 2002).

In the archaic *Homo* representatives (*H. ergaster*, *H. erectus*, Ceprano), the pattern displayed by frontal morphology combines with a posterior projection of the occipital torus and a backward orientation of the inion. As this anatomical region is functionally associated with the

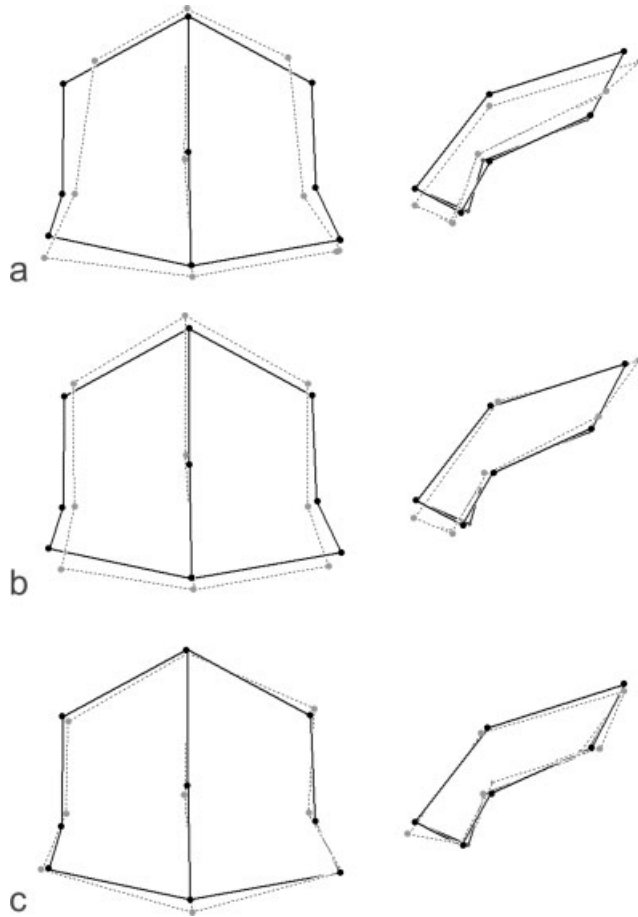


Fig. 9. The Ceprano configuration is superimposed and compared with the average shape from (a) early *Homo* (KNM-ER1813, KNM-ER 3733, KNM-ER 3883, Dmanisi 2280), (b) Asian *Homo erectus* (Zhoukoudian 3, Zhoukoudian 11, Ngandong 12, Sambungmacan 3), and (c) *Homo heidelbergensis/rhodesiensis* (Kabwe, Bodo, Petralona), in frontal (left) and left lateral (right) view; Ceprano is shown with solid links, the target shapes are shown with dotted links.

nuchal muscles (most of all: *trapezius*, *sternocleidomastoideus*, *splenius capitis*, *semispinalis capitis*) and with head posture and balance, the relationship between nuchal morphology, supraorbital structures, and face/vault topology should be considered an interesting topic for further biomechanical investigations. When the limited variation of the midsagittal endocranial frontal profile among the genus *Homo* (Bookstein et al., 1999) is taken into account, the ectocranial changes between archaic and more derived *taxa* should be interpreted in terms of structural network (*sensu* Moss and Young, 1960), rather than in terms of phylogeny *per se*. The physical environment and developmental relationships between the anatomical structures (muscles, tendons, bones) generate a biomechanical system that is very useful to describe morphology according to functions, physiological responses, or constraints. At the same time, this network often hampers a useful recognition of the cause/consequence patterns, rarely providing direct and linear evidence of phylogenetic trends. Phylogenetic and structural signals act together to shape morphology, possibly confounding the final inferences. For example, it is worth noting that, although the occipital ectocranial

morphology of Ceprano has affinities with *H. ergaster/erectus*, its occipital lobes—and, consequently, the endocranial shape—do not show the backward projection described in many Asian *H. erectus* specimens (Bruner, 2004; Bruner and Manzi, 2005).

The cranial vault shape is directly related to the encephalic development (Moss and Young, 1960; Enlow, 1990). Accordingly, the first axis of variation in the shape space of our analytical framework appears to be strongly connected with the flattening/enlargement of the parietal lobes which, in turn, have been described as major determinants within the evolution of the human brain (Bruner et al., 2003; Bruner, 2004). It is necessary to stress the fact that the midsagittal landmarks of Ceprano were partially extrapolated from the available profile. In the introduction to this paper we reported that the vault of Ceprano should have undergone a diagenetic warp that mainly affected the parietal areas and was probably due to a diagonal pressure acting upon the left parietal area, downward and heterolaterally. This deformation could have reduced the vertical diameters slightly. Nevertheless, the superimpositions suggest that Ceprano presently shows a more flattened vault than the *H. ergaster/erectus* comparisons. Therefore, if we assume there was a moderately higher vertical development of the calvarium, the original phenotype should have been even more similar to these specimens for this component of the outline.

By contrast, the 3D analysis of the frontal bone gives a rather different picture with respect to the result provided by the midsagittal profile. While our first analysis (including the frontal outline) shows an archaic geometry in Ceprano, the overall 3D shape of the frontal bone indicates clear differences with respect to early *Homo* representatives. In this analysis, a hypothetical plesiomorph morphology is shared by specimens referred to the *H. habilis* and *H. ergaster* hypodigms, with the frontal bone of KNM-ER 3733 and KNM-ER 3883 displaying only minor differences from KNM-ER1813 and Dmanisi 2280. Considering the current configuration of landmarks, all the other specimens (including Ceprano) show a different frontal shape, without displaying clear within-group differences related to chronology, geography, or taxonomy. This might suggest a low resolution of the geometrical model involved, but it may also imply a minor variation in the frontal bone shape—except for the mentioned morphology of the browridges, which is not included in the analysis—among the derived *Homo taxa*. Actually, rather than depending upon local shape changes, the differences in the frontal morphology appears mainly associated with the orientation of the bone with respect to the entire skull. As mentioned, the midsagittal shape of the inner table is rather constant in both archaic and modern humans (Bookstein et al., 1999). Changes involving the frontal lobes are only related to a minor allometric elevation and widening, with a rotation of their position with respect to the neurocranial longitudinal axis, in accordance with relative changes (shortening or enlargement) of the parietal lobes (Bruner, 2004). Thus, the derived human morphs show a tendency toward a vertical development of the entire frontal bone associated with a relative enlargement of the squama, which, in turn, is described by the widening of the bistephanic breadth. Both processes (vertical development and widening of the squama) may be described in relation to endocranial variations (i.e., shape changes of the frontal lobes).

In this perspective, the genus *Homo* may be divided between those morphs with wide frontal lobes, both in relative and absolute terms (Neandertals and modern humans), and those with relatively narrow frontal lobes (early *Homo* and *H. erectus*), while *H. heidelbergensis* displays a more heterogeneous range of variation. Nevertheless, no data is able at present to reject the hypothesis of a shared allometric pattern for the enlargement of the frontal areas. Particularly, Ceprano shows a clear and marked widening of the frontal lobes (not biased by the diagenetic distortion). This condition detaches the endocranial frontal shape of Ceprano from early *Homo* as well as from the Asian *H. erectus* variation and may be considered responsible for its ectocranial morphology, which separates this specimen from the morphology of early *Homo* representatives.

The phenotypic affinity in frontal shape between Ceprano and Middle Pleistocene specimens such as Petralona, Kabwe, and Bodo, requires further attention. According to the cophenetic correlation coefficients obtained with the two cluster procedures, the morphological signal related to the frontal shape is less defined than the signal provided by the previous analysis (midsagittal profile). This involves a higher ratio of within and between *taxa* variation, namely large differences between individuals and small differences between *taxa*. Therefore, the phenogram describes the general affinities adequately, but may be influenced by minor variations in individual specimens, without any particular phylogenetic meaning. It is therefore more informative that, according to the major trends displayed by the first two principal components, Ceprano occupies a position closer to the African Middle Pleistocene sample than to other specimens. These fossils share median values for the first component, and large values for the second one. That is, they all have relative short and wide frontal bones compared to specimens assigned to *H. erectus* s.s., *H. neanderthalensis*, or *H. sapiens*: the position of the bregma is more advanced, and the frontal squama appears therefore relatively less elongated and wider.

Differences between Ceprano and *H. heidelbergensis/rhodesiensis* in the relationship between frontal squama and supraorbital torus have been described elsewhere (Bruner and Manzi, 2005), and the morphological affinities with the same specimens in terms of the general morphology of the browridge were also described (Manzi et al., 2001). Ceprano shows a double-arched superior profile, while it is almost rectilinear inferiorly, and displays a phenotypic torsion also present in Kabwe, Bodo, Petralona, and other Middle Pleistocene humans from Africa and Europe. In this respect, we disagree somewhat with interpretations of the frontal bone of the same group of specimens as less derived (Rightmire, 2001), and suggest that the frontal bone morphology is able to provide both phylogenetic and structural information on the evolutionary dynamics among the genus *Homo*.

CONCLUSIONS

Morphology and shape analysis are but a complementary tool in approaching phylogeny and evolutionary dynamics. Taking into account the inconstant relationships between morphological variations and taxonomy (Tattersall, 1986; Turner, 1986; Lieberman, 1995, 1999; Collard and Wood, 2000; Plavcan and Cope, 2001), the data discussed here describe and quantify the degree

of phenetic similarity/differences associated with the unique pattern of cranial morphology displayed by Ceprano, when the available (nondistorted) evidence is considered. This calvarium shares the same pattern of midsagittal profile with more archaic humans (*H. ergaster*, *H. erectus*), including the shape of the supraorbital and nugal structures. In contrast, it displays major differences in the architecture of the frontal bone when compared to *H. habilis* and *H. ergaster*, and in the proportions of the frontal squama when compared to Asian *H. erectus*. In comparison with the morphology of the samples referred to *H. heidelbergensis/rhodesiensis*, Ceprano shows a similar shape of the frontal bone, a common (and probably derived) morphology of the browridge, but a different relationship between the frontal torus and squama. The combination of these data suggests that an appropriate taxonomic interpretation of the Italian specimen cannot be referred to the *taxa* *H. ergaster* or *H. erectus*, but that a distinct archaic cluster of the genus *Homo* should be considered, either as a distinct species or, alternatively, as an ancestral morphotype of the *H. heidelbergensis/rhodesiensis* hypodigm.

Therefore, the morphological distinctiveness of Ceprano as well as its mosaic of plesiomorph and derived traits—described here within the formal framework provided by geometric morphometric—together with the geo-chronological context of the Italian specimen do not falsify the hypothesis about a possible role as phenetic and (possibly) phylogenetic link between early *Homo* and the Middle Pleistocene populations of Europe and Africa (Manzi et al., 2001). Nevertheless, a definite taxonomic interpretation of this fossil cannot be provided until more appropriate comparative fossil samples (both in terms of chronology and anatomical completeness) are recovered.

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