

CT-Based Description and Phyletic Evaluation of the Archaic Human Calvarium From Ceprano, Italy

EMILIANO BRUNER^{1,2} AND GIORGIO MANZI^{1,2*}

¹Dipartimento di Biologia Animale e dell'Uomo, Università La Sapienza, Rome, Italy

²Istituto Italiano di Paleontologia Umana, Rome, Italy

ABSTRACT

The discovery in 1994, of a fossilized human calvarium near Ceprano, Italy, dated about 800–900 thousand years before present, opened a new page for the study of human evolution in Europe. It extended the continental fossil record over the boundary between Early and Middle Pleistocene for the first time and revealed the cranial morphology of humans that were probably ancestral to both Neanderthals and modern *Homo sapiens*. A tomographic analysis of the Italian specimen is reported here in order to describe size and shape, vascular traces, and other features of the endocranium, as well as some relevant ectocranial traits (particularly of the frontal region). Our results show that the Ceprano calvarium displays plesiomorphies shared by early *Homo* taxa, involving a general archaic phenotype. At the same time, the presence of some derived features suggests a phylogenetic relationship with the populations referred to the subsequent polymorphic species *H. heidelbergensis*. The morphology of the supraorbital structures is different from the double-arched browridge of the African *H. ergaster*, while its superior shape shows similarities with African Middle Pleistocene specimens (Bodo, Kabwe). In contrast, the relationship between supraorbital torus and frontal squama points to an archaic pattern of the relationship between face and vault, associated to moderately narrow frontal lobes and limited development of the upper parietal areas. Despite a nonderived endocranial shape, the increase of cranial capacity (related to a general endocranial widening) and the probable absence of a clear occipital projection also suggest an evolutionary independence from the Asian *H. erectus* lineage. This analysis therefore supports the conclusion that the Ceprano calvarium represents the best available candidate for the ancestral phenotype of the cranial variation observed among Middle Pleistocene fossil samples in Africa and Europe. Nevertheless, a proper taxonomic interpretation of this crucial specimen remains puzzling. © 2005 Wiley-Liss, Inc.

Key words: paleoanthropology; cranial morphology; computed tomography; endocranial features; human evolution

Several fragments of a fossil human cranium were found in March 1994 near the town of Ceprano, about 100 km southeast of Rome in central Italy (Fig. 1; compare, e.g., Ascenzi et al., 1996). After the fragments were physically reassembled (see below for a few details about the reconstruction and references), a rather complete, archaic-looking calvarium became available for investigation. Unfortunately, it was missing a great part of the face and portions of the cranial base.

The specimen was discovered as a result of systematic surveys conducted for decades in the region by the Istituto Italiano di Paleontologia Umana (IsIPU). The paleontological and archeological knowledge previously acquired about the Ceprano basin, combined with a geostratigraphic evaluation of the site itself, allowed A.G. Segre (Ascenzi et al., 1996, 2000; Ascenzi and Segre, 1997a) to

attribute the chronology of the cranium to more than 700 thousand years before present (kyr BP), more probably to the range 800–900 kyr BP. A stratigraphic column based

Grant sponsor: the Italian Ministero per i Beni Culturali e Ambientali; Grant sponsor: the Italian Ministero per l'Istruzione, Università e Ricerca.

*Correspondence to: Giorgio Manzi, Dipartimento di Biologia Animale e dell'Uomo, Università La Sapienza, P. le A. Moro 5, 00185 Roma, Italy. Fax: 39-06-4991-2495. E-mail: giorgio.manzi@uniroma1.it

Received 26 October 2004; Accepted 28 February 2005

DOI 10.1002/ar.a.20205

Published online 9 June 2005 in Wiley InterScience (www.interscience.wiley.com).

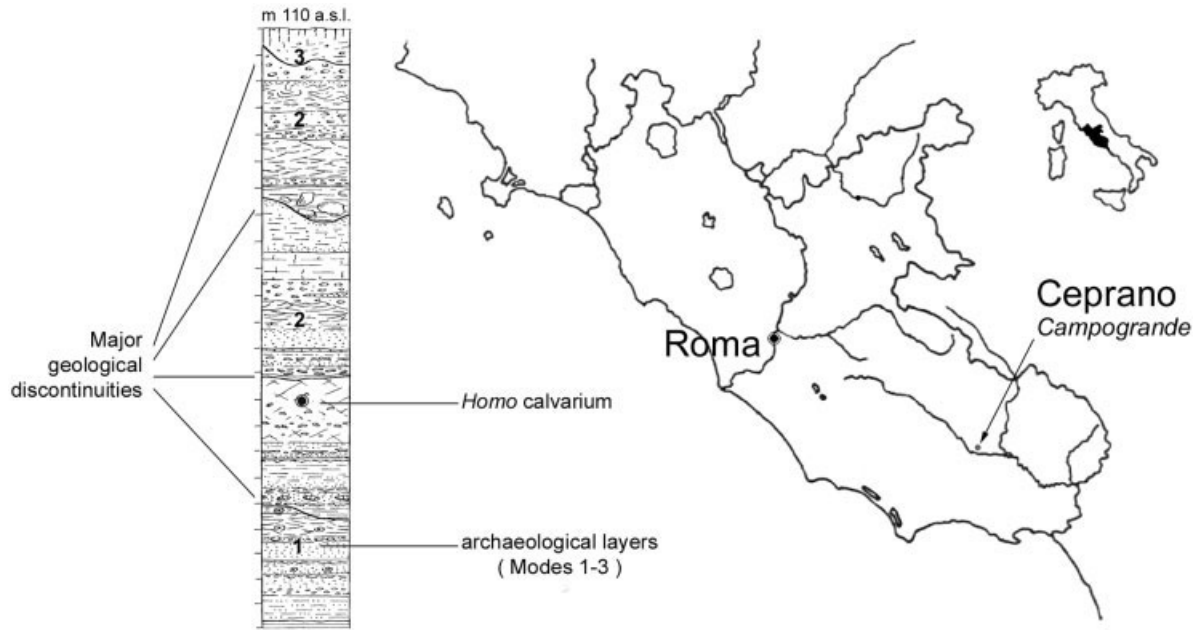


Fig. 1. Stratigraphic compilation column of the uppermost series in the Ceprano basin (left; after Ascenzi and Segre, 1997b) and geographical position of the Ceprano-Campogrande area within Latium, central Italy (right). Some relevant geoarcheological features are evidenced in the stratigraphy.

on regional correlations (Fig. 1) matches the position of the human specimen in a time span bracketed between the more recent volcanic activity known in the area—whose oldest occurrence is radiometrically referred to about 700 kyr BP (Fornaseri, 1985)—and more ancient volcanoclastic sands, K/Ar dated to $1,060 \pm 110$ kyr BP (Sevink et al., 1984). Furthermore, it is hypothesized that the inclusion of the cranium in the clay stratum where it has been discovered was subsequent to its fossilization in other and more ancient deposits (Ascenzi and Segre, 1997b). Thus, given the probable secondary nature of its deposition, the association of the cranium with pebble/flakes assemblages discovered in other sites of the Ceprano basin may be hypothesized. Special reference must be made to the “mode 1” Paleolithic material coming from Castro dei Volsci, with abundant flakes in silex and choppers in quartzite (Biddittu, 1974, 1984; Ascenzi and Segre, 1997b). Further elements are expected in the near future, given that systematic excavations started recently in the area (Biddittu et al., 2002, 2004), with the aim both to ascertain details of the stratigraphic sequence and to add evidence to the paleontological and archeological record.

The taxonomic position of Ceprano is not obvious, although this argument has been tentatively addressed in a number of papers, ranging from the original acknowledgment of the cranium as “late” *H. erectus* (Ascenzi et al., 1996) to more recent reappraisals. Among other hypotheses, the Italian specimen may be regarded as a variety of the species *H. antecessor* (e.g., Manzi et al., 2001a; Manzi, 2004), named after the penecontemporaneous Spanish sample from Atapuerca TD6 (Bermúdez de Castro et al., 1997). A new species name has also been suggested on the basis of the Ceprano calvarium alone, perhaps with the aim to emphasize its peculiar features (Mallegni et al., 2003).

Nevertheless, in view of its dating, geographic position, and morphology, Ceprano represents a crucial specimen to investigate the relationships among extinct *Homo* species (or varieties; compare, e.g., Antón, 2003) between Early and Middle Pleistocene. The calvarium displays several plesiomorphic features, which lead to a general resemblance to archaic morphotypes such as those included in the hypodigms of *H. ergaster* (Africa) and *H. erectus* (Eastern Asia), hereafter broadly referred to as *H. erectus sensu lato* (*s.l.*). At the same time, Ceprano shares a number of apomorphic traits with Middle Pleistocene Afro-European humans, usually included within the polymorphic species *H. heidelbergensis* (e.g., Rightmire, 1998).

When this combination of archaic and derived features is considered, the Italian specimen may be regarded as a phenotypic and possibly phylogenetic bridge between early representatives of the genus *Homo* and the subsequent Afro-European variability. Particularly, some affinities have been pointed out, especially for traits of the frontal region, with the African fossil record (Manzi et al., 2001a; Mallegni et al., 2003), in both its late Early Pleistocene (e.g., OH9, Daka, Buia) and early Middle Pleistocene (e.g., Bodo, Kabwe, Saldanha) segments of variation, regardless of whether these hominines are assumed to be in a direct phyletic connection or not (Asfaw et al., 2002; Manzi et al., 2003).

In this article, we provide a detailed description of the Ceprano calvarium, enhanced by imaging techniques. In the last decade, computed tomography (CT) has been successfully applied to paleoanthropology. Combined with digital morphology and geometric morphometrics (e.g., Zollikofer et al., 1998; Recheis et al., 1999a; Spoor et al., 2000a, 2000b), it allows for enhanced access to several unexplored volumes and surfaces. Considering the preservation of each fossil specimen, these techniques can be

used to describe features such as the inner bony layers, pneumatization, semicircular canals, frontal sinuses, and general endocranial shape. Our main goal, therefore, is to consider critically the morphology of Ceprano, with special reference to its internal structures, and to compare some of these features with other related specimens.

The morphology of the supraorbital region and other traits are compared with the two fossil crania from east Africa available at present for digital morphological analysis: the Olduvai hominid 9 (OH9) and the Middle Awash specimen from Bodo (Seidler et al., 1999; Weber et al., 2003). These represent two distinct poles of variation along the hypothetical African lineage mentioned above. The former specimen, OH9, is referred to 1.4–1.2 Myr BP ca. and displays several of *H. erectus s.l.* features (see Schwartz and Tattersall, 2003), while Bodo is an early Middle Pleistocene specimen, dated around 600 kyr BP, who is considered a significant reference for the cranial morphology of *H. heidelbergensis* (Rightmire, 1996; Conroy et al., 2000). Therefore, both the specimens have been considered as good comparative test cases because of their common digital availability, chronology (bracketing the Matuyama-Brunhes boundary), geographical localization in Africa, and diverse taxonomic status, probably associated with different phylogenetic processes. Other comparative samples are also considered, making special reference to the African Middle Pleistocene specimen from Kabwe (formerly known as Broken Hill, Zambia), holotype of *H. rhodesiensis*, but more commonly referred at the moment to *H. heidelbergensis*.

MATERIALS AND METHODS

The present reconstruction of the Ceprano calvarium (CPR) is the result of a process that started with the original work by A. Ascenzi et al. (1996), subsequently improved by R.J. Clarke (2000; see also Ascenzi and Segre, 2000), and further revised by M.A. de Lumley and F. Mallegni (Ascenzi et al., 2000). CPR is represented by the incomplete anterior portions, including frontal bone, frontal processes of both the zygomatic bones, and part of the sphenoid, while the posterior portions are composed of the right parietal, the largely preserved occipital bone, important portions of both temporals, and fragments of the left parietal. As described extensively elsewhere (e.g., Ascenzi et al., 1996; Manzi et al., 2001a), the specimen is platycephalic and elongated anteroposteriorly (a-p), with the maximum length between glabella and inion, while it shows a considerable widening of the posterolateral aspect of the braincase. The maximum breadth is low, at the level of the supramastoid crests. The bone thickness is exceptional, a value of 16 mm being recorded at the right parietal eminence.

The calvarium has been CT-scanned with a Tomoscan AUEP Philips by sequential and contiguous 1 mm slices, at 25 mA and 140 kV, using a 512 × 512 matrix with a resolution of 0.40 mm/pixel, without filtering it or using a gantry tilt. Although more recent medical and industrial CT can now be used to obtain higher-resolution images, slices of 1 mm can allow for a useful and insightful reconstruction of the main anatomical structures considered in this analysis such as endocranial surfaces, sinuses, or supraorbital morphology (Spoor et al., 2000a, 2000b). A transversal scan plane was used, approaching the Frankfurt horizontal. This plane can be only tentatively extrapolated in this specimen, however, due to the lack of the

inferior orbital rim. Data have been exported as Dicom files, and the CT analysis was performed using Mimics 7.0 (Materialise). The Hounsfield scale was used to display the attenuation coefficients, ranging from 0 to 4,096 Hounsfield units (Hu). The attenuation spectrum was computed as the abundance of each given gray value to check the densitometric composition of the entire specimen. The anatomy and morphology of the inner structures have been considered using the CT slices and the three-dimensional rendering after segmentation of each layer. Scout views by sum of gray values and upper projection have been computed by ImageJ (<http://rsb.info.nih.gov/ij/>).

Some major diameters have been used to describe the endocranial morphology (for details, see Bruner et al., 2003a): hemispheric length (HL; from the most anterior point of the frontal lobe to the most posterior point of the occipital lobe; averaged hemispheres), endocranial maximum width (MW; orthogonal to the midsagittal plane), frontal width (BW; between Broca's caps, at the most lateral points of the base of the third frontal circumvolution), and endocranial vault height (VH; calculated orthogonally at the 50% of the fronto-occipital chord). The frontal width in CPR has been obtained by doubling the value obtained for the right hemisphere missing the bony surface pertinent to the heterolateral one.

Comparative morphometric data have been sampled from the endocast collections at the Museo di Antropologia "G. Sergi" (Rome, Italy), the Istituto Italiano di Paleontologia Umana (Rome, Italy), the Institut de Paléontologie Humaine (Paris, France), and the Universidad Complutense (Madrid, Spain). Tomographic data from OH9 and Bodo (Seidler et al., 1999; Weber et al., 2003) were segmented and analyzed using Mimics 7.0.

A brief review of the condition of CPR is warranted here, particularly in light of its fragmented, incomplete, and partially distorted condition. It has been hypothesized elsewhere (e.g., Manzi, 2004) that a main diagenetic deformation of the specimen is represented by a lateral downward pressure applied onto the left parietal, which became flattened and medially deflected. Consequently, the heterolateral wall of the neurocranium has been warped laterally and is now more vertical and angled than it was originally. If this hypothesis is correct, we may make the following assumptions. First, it is probable that both the frontal breadth and the hemispheric length are not affected by this process. Second, the absolute value of the main endocranial breadth should not be involved in this change, since the coronal surface of the cranium was simply shifted toward the right side. Third, the endocranial height might be slightly reduced as a consequence of the downward vault flattening on the left side.

A graphical warping of the main laterolateral deformation in CPR was computed using a landmark-based superimposition approach to attempt this problem. A coronal CT section that preserves a good percentage of the endocranial outline (approximately corresponding to the level of the maximum ectocranial breadth, which includes the supramastoid crests) was divided into its left and right components with respect to the midsagittal plane (Fig. 2). The missing fractions of the outline were visually optimized following a reasonable minimum bending profile, in which three points available along the preserved endocranial surface were used to infer the missing coronal sections. Each endocranial half-profile has been reduced to an equally spaced 50-landmark configuration by tpsDig 1.20

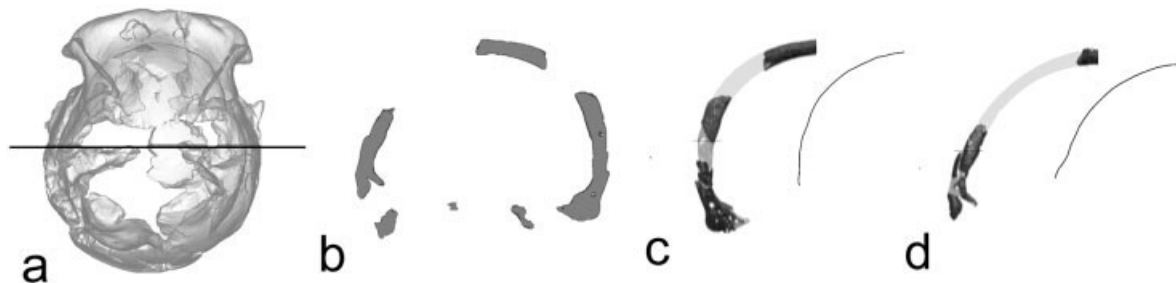


Fig. 2. Reconstruction of the CPR coronal profile. A digital section approaching the maximum width (a) was isolated (b) and used to outline the right (c) and left (d) endocranial profiles. These profiles were reduced to a 50-semilandmark configuration and superimposed according to the Procrustes procedure to compute a consensus average shape. The original tomographic slice was then warped into the averaged shape.

(Rohlf, 1998). After mirror imaging, the two configurations were superimposed using the Procrustes procedure—centroid translation, size normalization, and least-square rotation (Bookstein, 1991)—and then warped into the consensus average shape by tpsSuper 1.07 (Rohlf, 2000).

RESULTS

CT Data and Digital Survey

The CT scan and segmentation of CPR was performed without technical difficulties (Fig. 3). Even if the calvarium is heavily fossilized, the lack of filled volumes and large masses prevented streak artifacts caused by lack of detector signal or beam hardening (Spoor et al., 2000a, 2000b). Furthermore, no overflow was recorded. The attenuation spectrum of the fossil (Fig. 4) shows a biphasic distribution, with two densitometric components partially distinguishable at about 2,500 Hu. The most dense phase (Hu 3210 ± 356 SD) is related to the fossil component, while the lower peak (Hu 1883 ± 407 SD) mostly represents the artificial material (plaster of paris) that was used for insertions in the physical reconstruction, plus a certain amount of partial volume effect (see Spoor et al., 2000a, 2000b) possibly due to the large extension of some diploic volumes.

Radiographic techniques such as computed tomography can be extremely useful to check the relationship between the fossil bone and geological matrices (e.g., Recheis et al., 1999b; Manzi et al., 2001b; Prossinger et al., 2003) or to consider the presence of fractures and areas of fragility (e.g., Wind, 1984; Bruner and Manzi, 2003). Clearly, this knowledge is necessary in order to assess the preservation of the specimen and to evaluate its reconstruction from fragmentary remains. The tomographic analysis of the CPR calvarium allows us to emphasize some major points in this regard. First, the comparison between the endocranial and ectocranial surfaces shows some limits in the present reconstruction. The orientation of the pyramids is different and probably biased, with bony fragments juxtaposed within a rather amorphous matrix. In addition, the tomographic slices show that some minor mistakes in the juxtaposition of other fossil fragments appear to have occurred, particularly at the left posterior border of the anterior fossa. It is also possible that the lack of local correspondences produced some major inaccuracy in the positioning of the bones. Despite the fact that part of these

biases may not have been caused by the reconstruction itself, but may be related to diagenetic pressures, it is necessary to consider the relationship between superficial and deep layers for a correct interpretation, which will be adequately achieved only using a digital approach. Second, we observe that, in general, the fossil volumes and surfaces are well recognizable from the artificial inclusions. However, the overlap occurring between the two phases indicates a certain percentage of melted matrices that are densitometrically unsolvable. Such an overlap between fossil bone and plaster insertions, especially localized in the area of the temporal pyramids, emphasizes the irreversibility of this kind of reconstructions, when these are based on the combination between the original fragments and artificial materials that are densitometrically similar to the fossil matrix. Conversely, reconstruction based on casts and/or using digital and noninvasive procedures are definitely preferable.

As shown in Figure 5, the result of the superimposition and warping of the best preserved half coronal outlines (compare Fig. 2) showed that the consensus average shape of the CPR cranial vault exhibits a low-positioned maximum endocranial breadth, with nonparallel and divergent parietal walls. Thus, assuming a comparable but opposite deformation on the two sides, the mean configuration obtained here may give a plausible yet preliminary approximation to the original endocranial shape at the given coronal level. In any case, in view of the fragmentary nature of the cranium and the inferences applied to the reconstruction of the missing areas, these conclusions should be viewed as merely explorative.

Supraorbital Torus and Frontal Sinuses

As already reported elsewhere (e.g., Manzi et al., 2001a), the frontal torus of CPR is remarkably developed (Fig. 3). It shows a depressed median area in both frontal (glabellar depression) and superior position (supraglabellar depression). Despite the visible trauma affecting the superior-lateral aspect of the right browridge (Ascenzi et al., 1996; Ascenzi and Segre, 1997b), the torus appears quite symmetrical and only hypertrophic around the area where the injury occurred. The browridge is well developed, expanding laterally on both sides. The supraorbital structures show variable vertical thickness across their mediolateral extension, where height grows steeply from the midsagittal plane, reaching its maximum value (21

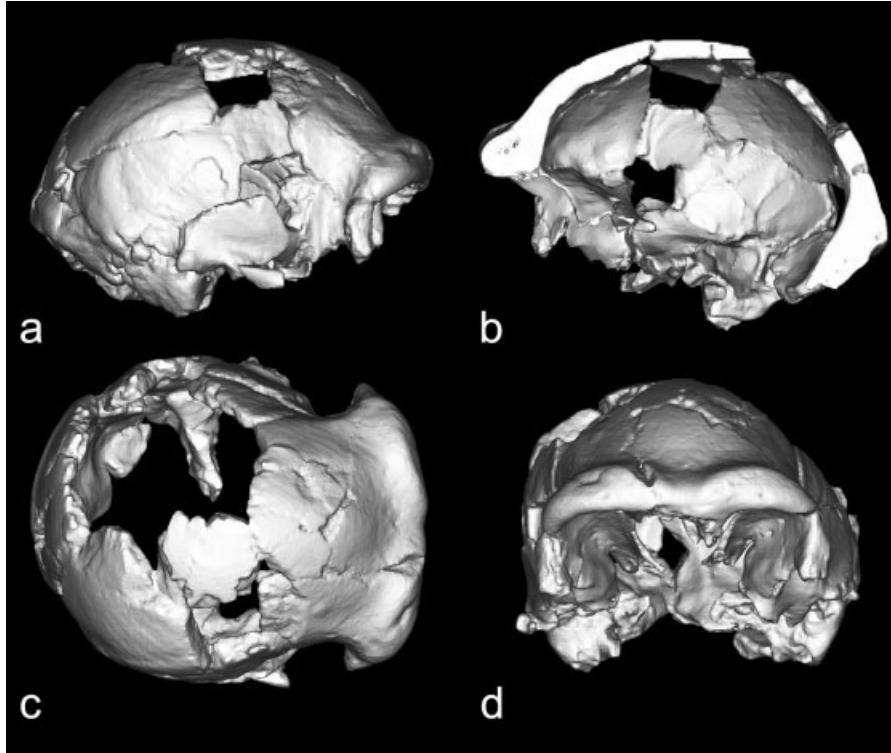


Fig. 3. Digital reconstruction of the CPR calvarium: right lateral view (a), right half-midsagittal section (b), dorsal view (c), and frontal view (d).

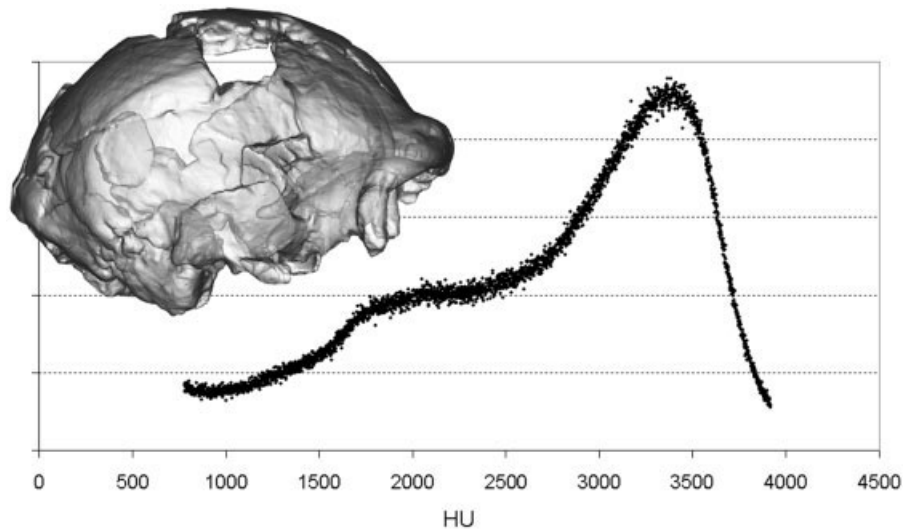


Fig. 4. The attenuation spectrum of the CPR calvarium, showing a biphasic distribution (HU: Hounsfield units). The low-density phase represents plaster and partial volume effect. The highest density phase represents the fossil bone. The digital replica of the CPR calvarium shows the skull in lateral view (transparency added).

mm) around midline of each orbit, and gradually decreases laterally. At the same time, the inferior outline (i.e., the superior border of the orbits) is almost rectilinear in frontal view, contrasting visibly with the arched appearance of the uppermost profile of each torus. A distinc-

tive feature is also the twisted appearance (or mid-orbit torsion) of the external aspect of each supraorbital surface. This displays a flat and vermiculate medial component that, in turn, is clearly distinguishable from the more rounded and bulging lateral part.

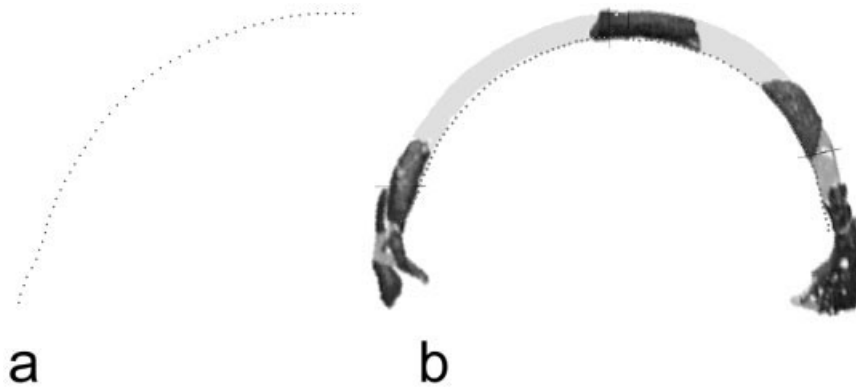


Fig. 5. Consensus average shape computed by Procrustes superimposition of the right and left coronal profile (a) and warping of the entire tomographic slice (b).

Computed tomography allows a detailed approach to the supraorbital region as far as the morphology of the internal volumes is concerned, helping to add further insight to previous descriptions (e.g., Ascenzi et al., 1996; Manzi et al., 2001). When a midsagittal section is observed in lateral view (Fig. 3b), the extension of the frontal torus of CPR is noticeable, in relation to both the occurrence of a well-defined supratoral sulcus and a receding but rather bulging squama. As shown in Figure 6, the posterior displacement of the frontal lobes, which clearly lie behind the orbital roofs, is also considerable.

The torus of CPR, filled with spongy tissue, appears as an extremely developed structure in transversal sections, too (Fig. 7). Laterally, it shows a marked forward projection of the browridges, which leads to a gradual increase of the a-p thickness of the torus moving from the midsagittal plane toward more lateral sections. This variable a-p depth is related to the greater curvature of the endocranial shape compared to the profile of the ectocranial surface, which is in turn due to the narrowing of the frontal lobes on one side, and to the moderate extension of the glabella region on the other.

In CPR, the torus includes the two frontal sinuses into the extended diploic volume (Fig. 8). The sinuses are well defined on both sides, although they are asymmetric. Neither the left nor the right sinus reaches the median area. As a matter of fact, they are not separated by a thin septum, but by a large spongy region of about 14 mm. Given the definite morphology of both sinuses, this asymmetry does not appear due to internal remodeling of the torus consequent to the trauma well visible on the ectocranial surface of the right browridge. The left sinus (16 mm length, 23 mm width, 11 mm height), larger than the right one, is formed by two superior and one inferior chambers. The larger median upper chamber originates from the inferior one, which in turn is continuous with the paranasal sinuses. The lateral extension of this sinus reaches the medial third of the orbital width. The right one is definitely smaller (9 mm length, 14 mm width, 9 mm height); it is limited in extension to the medial quarter of the orbital width. It is ovoidal and single-chambered, while a second, more medial and inferior compartment is continuous with the ethmoidal sinuses.

Endocranial Size and Shape

Considering the fragmentary and incomplete nature of the specimen, the reconstruction of a digital endocast (e.g., Tobias, 2001; Bruner, 2003) is rather unsuitable. In this case, the reconstruction would be based on interpolations and it would necessarily require a certain level of subjectivity, without any real improvement of the information already available. For the same reason, we do not provide any new evaluation of the CPR cranial capacity here, whose estimates based on the present reconstruction range between roughly 1,050 and 1,200 ml (Ascenzi and Segre, 2000; Mallegni et al., 2003).

Concerning general diameters, the hemispheric length of the CPR endocranium (157 mm) is comparable with values found in scarcely encephalized samples as those included in *H. erectus s.l.* (Fig. 9). The hemispheric length concerns the sagittal development of the brain and is a useful estimator of the basic encephalization degree. From this perspective, CPR may be referred to as a weakly encephalized morphotype compared to the *Homo* ranges of variation. At the same time, the endocranial vault height (68 mm) is similar to those of the European Würmian Neandertals, yet suggesting the absence of a pronounced platycephaly. Relatively to the hemispheric length, however, the vault appears high but not exceptional, showing a comparable value with specimens such as the relatively tall *H. erectus* Sambungmacan 3 endocast (Delson et al., 2001). Anyway, we have already pointed out that the vertical diameters are those that could have been more influenced by the diagenetic distortion and should be interpreted with some cautions.

The endocranium of CPR is definitely wide, when either its anterior and posterior diameters are considered, both in terms of absolute values and relatively to the endocranial length. The maximum width of CPR (139 mm) is comparable with the most encephalized morphs (Neandertals and modern humans), and even its frontal width (103 mm) is high. Anyway, compared to the hemispheric length, the respective residuals approach the 95% confidence ellipse of variation computed for the comparative sample (Fig. 9b and c). Similar figures are displayed by specimens such as Atapuerca-SH 4 and Guattari 1 for the frontal and maximum widths, respectively.

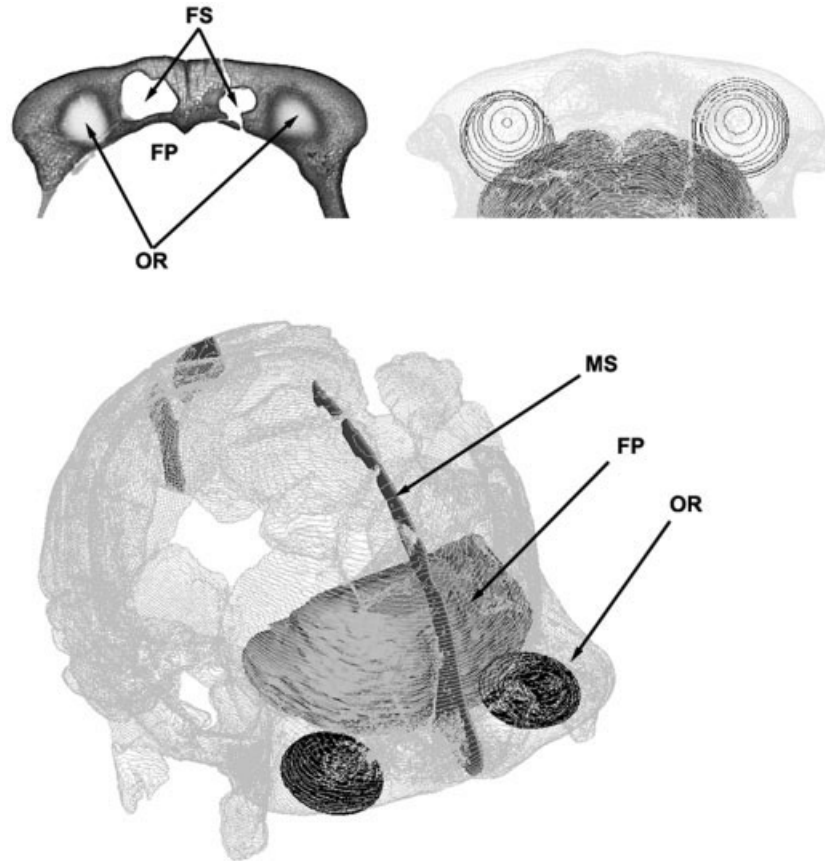


Fig. 6. The transversal CT slice (top left) and the three-dimensional rendering of the frontal area in upper view (top right) and of the entire skull in perspective (bottom) show the relative position of the orbital roofs (OR), frontal poles (FP), frontal sinuses (FS), and midsagittal section (MS).

The ratio between the frontal and maximum widths expresses the convergence of the frontal lobes anteriorly to the parietotemporal areas. Even if the cerebral breadths are widened compared to the archaic variation, CPR shows a frontal narrowing that approaches the pattern described in nonencephalized taxa (Fig. 9d).

The frontal asymmetries in CPR cannot be fully described because of the fractures and incompleteness of the left endocranial surface, which do not allow a standard metric comparison. However, the frontal lobes do not display visible differences in their longitudinal extension.

The parieto-occipital districts on the right hemisphere are more laterally developed than the counterparts, which appear in contrast a bit more elongated. The deformation of the vault does not allow the consideration of the exact development of the upper parietal districts. The occipital lobes taken as a whole are a-p-shortened, or (at least) not particularly extended backward. This region of the CPR endocast in fact displays neither a large projection behind the parietal-temporal complex, nor a flexion of the midsagittal profile around the perpendicular scissure, and the occipital lobes appear rather compressed onto the temporo-parietal ones.

Endocranial Vascular Traces

There is no evidence of the occurrence of a sphenoparietal (or Breschet) sinus. The trace of the superior sagittal

sinus runs at the torcular herophili into the left transverse sinus, and the ipsilateral sigmoid sinus is clearly enlarged when compared to the right one.

The path of the middle meningeal artery is well seen on the right hemisphere, in observing both the digital reconstruction and the fossil itself. The middle meningeal system of CPR is rather developed (Fig. 10), with a bregmatic ramus, that is relatively simple but not completely visible because of the fragmentation of the endocranial surface. Anyhow, the exact position of the respective bone fragment should be accurately reconsidered (M.H. Wolpoff, personal communication). The obelic ramus seems to derive from the anterior branch. Lacking the pertinent basal areas, it is actually close to the cross between the anterior and posterior branches, near the presumed position of the foramen spinosum, and should not be considered functionally related to the posterior vascular system. The obelic ramus is well developed, with two main bifurcations that are further branched, spreading on the parietal surface without anastomoses, and probably covering the supra-marginal and angular areas, respectively. The lambdatic ramus is quite simple and shows two large but short vessels.

Other Features

Pneumatized volumes can be localized in the temporal bones. The pyramids and mastoids are characterized by



Fig. 7. Tomographic sections of the supraorbital structures in Ceprano (a), Bodo (b), and Kabwe (c). Sections were computed approaching the glabella to show the frontal pneumatization, the morphology of the supraorbital torus, and the endocranial surface.

large and elongated cells, scattered and separated by thick bony layers (Fig. 11a). These volumes are strongly fragmented, fractured, and partly permeated by the artificial substance used in the reconstruction. The vestibular structures of the inner ear are not clearly identifiable. The right pyramids show a complete posterior semicircular canal, while the lateral one is just visible, but it is unfortunately in contact with the heavily damaged anterior areas. In the left side, traces of the inner ear structures are difficult to interpret. Although it is possible that analyses performed with higher-resolution techniques may be capable of yielding better digital results, the badly preserved and fractured condition of the vestibular structures of CPR will probably preclude our being able to assess its original morphology.

In addition, the vertical projection of the skull stresses the marked asymmetry in the orientation of the two temporal pyramids, the right one being strongly angled with respect to its counterpart. This difference is possibly related to the original physical assembling of the fragments, or to the diagenetic deformation of the calvarium itself. In any event, it must be carefully considered in case of future digital reconstructions.

The greater wings of the sphenoid show an extremely spongy volume on both sides (Fig. 11b). This pneumatization involves a considerable bulging of the associated orbital surfaces, which appear somewhat inflated. The diploic layers of the vault bones are visible, but it is not possible at present to localize a clear-cut distinction between the outer and inner tables.

DISCUSSION

Morphology of the Ceprano Calvarium

This article has described some anatomical features of the Ceprano calvarium through CT reconstruction in or-

der to better appreciate the distinctiveness of its ectocranial and endocranial morphology. In particular, we believe that valued insight has been offered in three areas: the missing facial and basal portions of CPR; comparative frontal morphology in archaic humans; and the encephalization process within the genus *Homo*.

The browridges in CPR are rather arched in their uppermost contour, but almost rectilinear inferiorly. This morphology should not be confused (contra Schwartz, 2004) with what is commonly described as “double-arched” shape of the supraorbital region taken as a whole. Absent in CPR, this is conversely the morphology we attribute to representatives of the Early Pleistocene African lineage (or *H. ergaster*), such as KNM-ER 3733 (Wood, 1991), or the partially described specimen from Buia (Abbate et al., 1998) and, above all, that from Bouri (or “Daka”; Asfaw et al., 2002). In these cases, the double-arched shape is clearly expressed and may be followed across the entire extension of the torus, from above the frontonasal suture toward the frontomale-orbitale. It also involves both the superior and inferior aspects of the browridges. By contrast, the straight inferior profile of the browridges is common among the Eastern Asian samples from Java and China, and its derived condition in *H. erectus* (sensu stricto) may be suggested. In this light, the variability described for the Dmanisi crania (Gabunia et al., 2000; Vekua et al., 2002) raises questions about the polarity of this combination of characters.

The ectocranial aspect of the supraorbital morphology in CPR may be assessed better through a direct comparison with OH9 and Bodo (Fig. 12). The torus in OH9 is different from CPR: it appears rather straight in frontal view (but a robust variant of the double-arched shape may be inferred), shows a constant vertical thickness, and lacks the mid-orbit torsion observed in CPR. By contrast, in Bodo a double-arched shape combines with the variable vertical thickness of each structure, producing lateral thinning, and with a weak mid-orbit torsion. Other Middle Pleistocene specimens, e.g., Arago, Kabwe, Saldanha, and possibly Petralona, exhibit the same combination of traits observed in Bodo. It is worth noting that the strongest similarity with CPR for mid-orbit torsion is found in Kabwe, as has been noted previously (e.g., Wolpoff, 2002). Whether or not this combination of traits (i.e., variable vertical thickness and associated mid-orbit torsion) may be assumed as derived in the Middle Pleistocene populations, for which CPR would thus represent an ancestral morphotype, requires further study.

Overall, the shape of the supraorbital region in the various specimens also appears characterized by the degree of inclusion of the browridges in the body of the frontal squama, that is, (ectocranially) by the presence/absence of a supratatorial sulcus (Fig. 13). In OH9 and in CPR, there is a marked flexion at the junction between the torus and the squama (independently from the depth of the sulcus), whereas in Bodo the midsagittal profile is continuous, lacking any appreciable depression. Kabwe shows a similar midsagittal continuity between the supraorbital structures and the frontal squama. Considering the comparable posterior position of the frontal lobes in CPR, Bodo, and Kabwe, this difference appears related to additional bony deposition in the supraorbital region of the two African specimens. Thus, differing from CPR, a midsagittal hypertrophy of the frontal squama in Bodo and Kabwe fills the space above the browridges (supra-

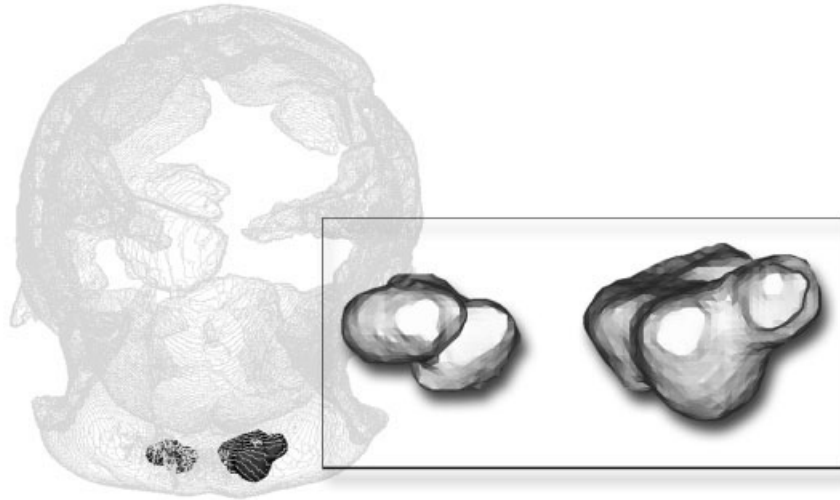


Fig. 8. Frontal sinuses in Ceprano in upper view. The left one is larger and formed by two upper chambers. The right one is smaller and formed by one single chamber. They are separated by a large bony volume. The polyline upper view of the CPR skull shows the relative position of the sinuses.

toral sulcus), including part of the torus into the squama. Interestingly, Petralona also shares the same frontal bone morphology noticed in the penecontemporaneous African crania (Stringer et al., 1979).

Endocranially, the posterior displacement of the frontal lobes observed in CPR is a feature that has already been described for massive Middle Pleistocene specimens such as Kabwe and Petralona (Seidler et al., 1997). This occurs also in Bodo and, more questionably (given the incompleteness of the specimen), in OH9. This seems to be a morphology shared by archaic specimens of the genus *Homo* in general, being the result of a combination between massive browridges and a receding frontal squama. It should be interpreted, therefore, as a structural consequence of such a shape of the forehead, without any peculiar phylogenetic meaning.

A certain stability of the midsagittal profile of the anterior fossa has been observed in comparing archaic and modern *Homo* (Bookstein et al., 1999). When the variation in the extension and morphology of the supraorbital region is considered, the posterior displacement of the frontal lobes shared among nonmodern specimens suggests a different relationship between neurocranium and splanchnocranium in archaic vs. modern humans as well as among different nonmodern specimens and/or taxa. In this framework, according to Lieberman (2000), the supraorbital torus may be viewed as a structural interface between neurocranium and splanchnocranium, being the result of the biomechanical interaction between the respective development pathways, and acting as a sort of hinge between vault and facial districts. In CPR, it might be inferred a different architecture of the cranium with respect to *H. heidelbergensis* representatives. Indeed, the coexistence of characters observed in *H. erectus s.l.* (relative independence between frontal torus and squama, narrowing of the frontal lobes,) with other features that are common in *H. heidelbergensis* (mid-orbit torsion and variable vertical thickness of the browridges) may imply in CPR a peculiar relationship between the braincase and the face.

Regarding internal structures of the torus (Fig. 14), CPR appears unique in its combination of features. OH9 is the specimen that shows the most massive volume when compared to the neurocranial dimensions (frontal lobes). As in CPR, we observe here a lateral increase of the a-p thickness of the torus that, however (differing from CPR), fills the structural gap due to very narrow frontal lobes, producing two expansions at the edges known as lateral wings (Macintosh and Larnack, 1972). By contrast, in Bodo and Kabwe the a-p thickness of the supraorbital torus is rather constant, associated to a relative widening of the frontal lobes and to a comparable curvature of the ectocranial (external profile of the browridges) vs. the endocranial (frontal lobes) outline. These Middle Pleistocene specimens also lack a clear midsagittal (glabellar) notch, which in contrast is present in OH9 and CPR.

The frontal sinuses in CPR are scarcely developed compared to the Middle Pleistocene range of variation (Seidler et al., 1997; Prossinger et al., 2003). It may be hypothesized that they cannot extend backward and upward, growing through the frontal bone, because of the structural independence between the supraorbital torus and the frontal squama mentioned above. Conversely, the continuity between squama and torus appears consistent with the development of the huge frontal pneumatization described for some Middle Pleistocene specimens, such as Steinheim, Petralona, and Kabwe, but lacking in the European Arago XXI (Seidler et al., 1997; Prossinger et al., 2003). In Bodo (Fig. 7), the frontal sinuses seem to show a morphology similar to Steinheim, Petralona, and Kabwe, although not clearly visible because of the permeation of geological matrices.

CPR shows small frontal sinuses compared also to those in modern humans (Weiglein, 1999). However, it must be noted that our knowledge on the heterogeneous variability of these traits is rather scarce (compare, e.g., Hauser and De Stefano, 1989), and also some robust fossil specimens of the Late Pleistocene and the Early Holocene have been respectively reported to display small (Bruner and Manzi, 2003) or almost absent (Bruner and Manzi, 2002) frontal sinuses.

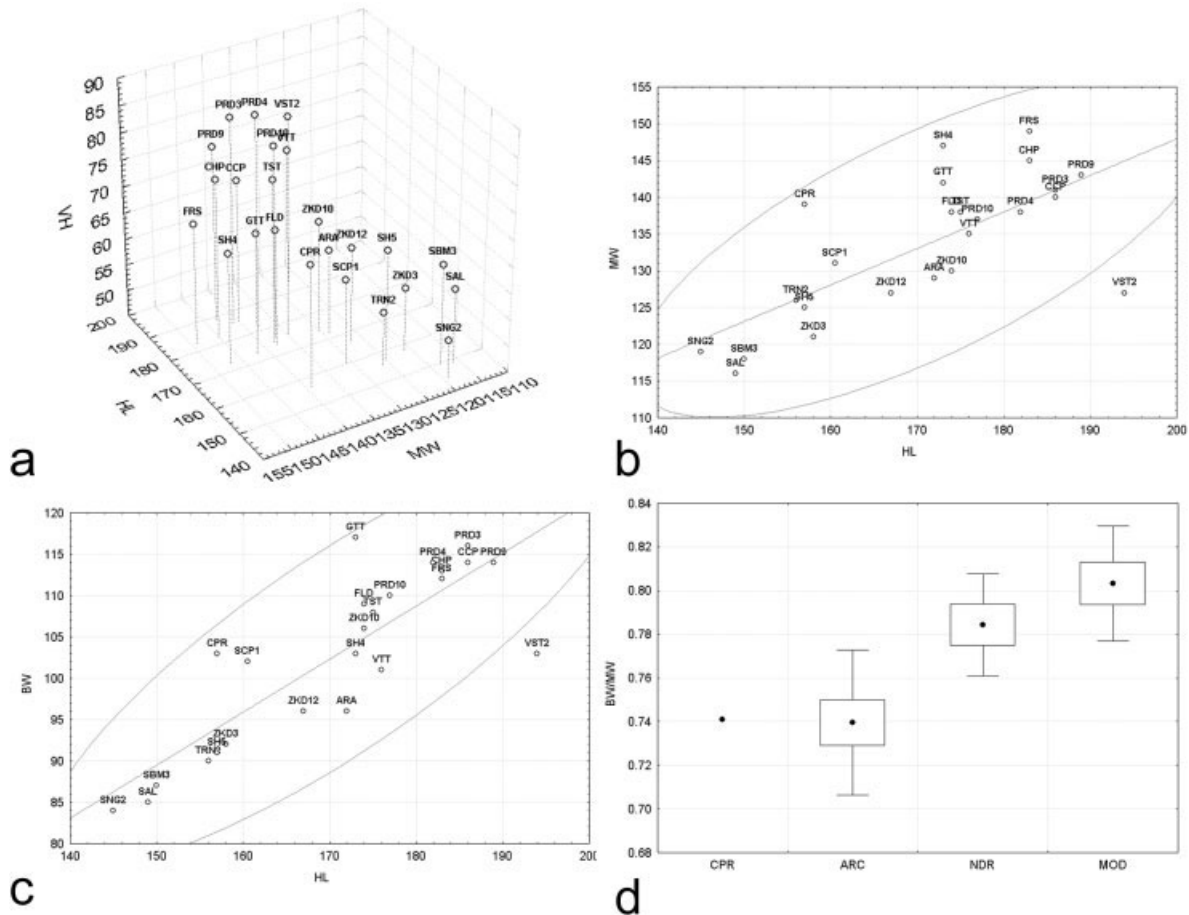


Fig. 9. Endocranial metric comparison. **a:** Maximum endocranial width (MW), hemispheric averaged length (HL), and vault height (VH). **b:** Hemispheric averaged length plotted onto maximum endocranial width. **c:** Hemispheric averaged length plotted onto maximum frontal width at the Broca's cap (BW). **d:** Mean, standard error, and standard deviation of the frontal/maximum widths ratio in modern humans (MOD), Neandertals (NDR), and *H. erectus/H. heidelbergensis* archaic group (ARC) compared

with the Ceperano (CPR) value. Specimen labels: SNG, Sangiran; TRN, Trnín; SAL, Salé; SBM, Sambungmacan; ZKD, Zhoukoudian; ARA, Arago; SH, Sima de los Huesos; SCP, Saccopastore; FLD, Feldhofer; TST, Tesik-Tash; CHP, La Chapelle-aux-Saints; FRS, La Ferrassie; CCP, Combe Capelle; PRD, Predmosti; VTT, Vatte di Zambana; VST, Vestonice.

When the variation in cranial capacity through Early and Middle Pleistocene is considered, two encephalization patterns have been described and were respectively related to the evolution of *Homo erectus s.l.* and of *Homo heidelbergensis* (Rightmire, 2004). The cranial capacity of CPR can only be estimated and probably ranges around 1,150 ml (cf. Ascenzi and Segre, 2000; Mallegni et al., 2003). Given the short hemispheric length of CPR, this relatively high endocranial volume may not be expected, while it is clearly associated to the considerable lateral enlargement of the specimen. However, although wide, the endocranium of CPR is not exceptional when compared to the variability of the genus *Homo* taken as a whole. The CPR endocranial width becomes exceptional when compared to the *H. erectus s.l.* variation. Actually, CPR is the only short-brained archaic specimen showing a large positive residual in the regression between hemispheric length and endocranial widths. If confirmed, this relationship would suggest that the CPR morphology is better interpreted within the evolutionary trajectory of

the Afro-European Middle Pleistocene lineage (or lineages), probably when it was still establishing.

As mentioned above, the frontal lobes of CPR show moderate lateral narrowing when viewed in transversal section and are compared to the posterior brain width. The coronal narrowing of the frontal areas with respect to the posterior breadth represents a morphology clearly expressed in small and short-brained specimens referred to *H. erectus s.l.*, while more encephalized taxa, including Neandertals and modern humans, show a relative frontal broadening (Grimaud-Hervé, 1997; Bruner et al., 2003a). Even Middle Pleistocene specimens like Bodo and Kabwe exhibit such derived condition.

The frontal broadening of the more encephalized taxa has been interpreted as the allometric variation along a shared structural trajectory within the genus *Homo*, related to splanchnocranial downward rotation and loadings onto the orbital roof (Bruner, 2004). If the endocranial width of CPR is not affected by the diagenetic distortion, the relative frontal narrowing (as ratio between anterior

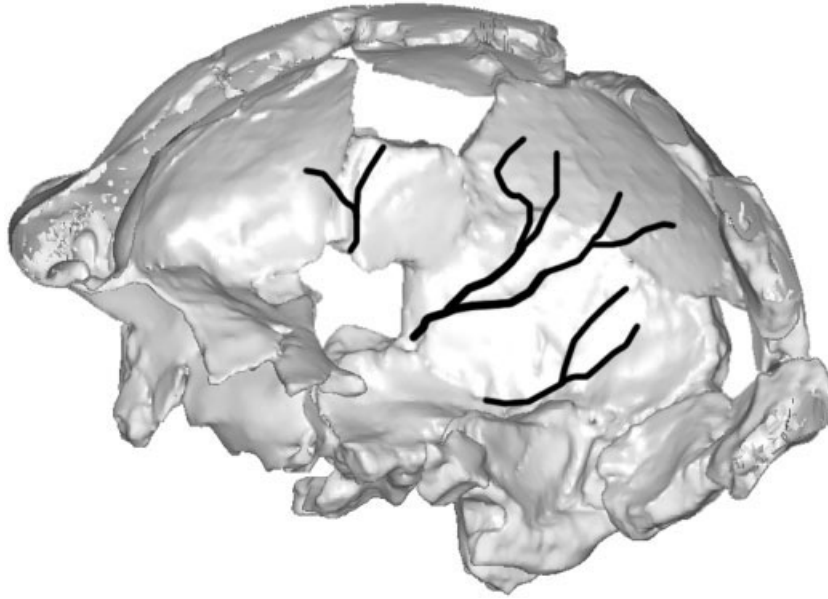


Fig. 10. Main traces of the middle meningeal vessels on the right hemisphere in CPR, shown on the sectioned digital replica.

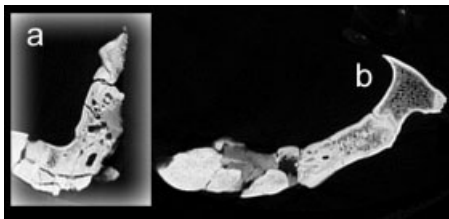


Fig. 11. Tomographic transversal sections showing pneumatic cells at the left temporal pyramids (a) and bony pneumatization at the ipsilateral sphenoid greater wing (b).

and posterior districts) is expected when a nonderived endocranial shape is maintained. Taking into account that the frontal areas have not likely been involved in the diagenetic deformation, this hypothesis must be considered. Interestingly, the early Neandertal cranium Saccopastore 1 shows a derived shape, i.e., a high anterior/posterior ratio of the brain widths or frontal relative broadening (data not shown), and a cranial capacity estimated at 1,174 cc (Sergi, 1944). The similar endocranial volume but different patterns in CPR (plesiomorph, *H. erectus*-like) and Saccopastore 1 (derived, Neandertal-like) suggest that a nonallometric (i.e., phylogenetic) role of the frontal lobe variation cannot be excluded. Alternatively, if the CPR endocranial width has been enlarged by the diagenetic pressure, the original anterior/posterior ratio may have been more similar to the pattern represented by Saccopastore. In this case, the hypothesis of a nonphylogenetic (i.e., size-related) frontal relative broadening has to be once more considered. Further considerations on the taphonomic processes involved in the CPR fossilization will help to improve this important issue.

One of the plesiomorphic features in CPR is the low-positioned maximum width of the endocranium, placed at the

level of the temporal lobes. This morphology is associated with the maximum ectocranial breadth in correspondence of the supramastoid crests (Ascenzi et al., 1996), and it is in accordance with the endocranial shape obtained after reduction of the probable diagenetic distortion by morphometric averaging the best preserved half coronal profiles (Fig. 5). The contour of the cranium in posterior view can be referred to as “low pentagonal” (according to the terminology used by Klein, 1999: p. 299): CPR does not display either the “globular” (or *en bombe*) Neandertal profile or the “intermediate pentagonal” pattern shared by Afro-European Middle Pleistocene morphotypes, or even the “high pentagonal” shape that is common among modern humans. Thus, as in *H. erectus s.l.* (e.g., Grimaud-Hervé, 1997), CPR does not show any relevant parasagittal parietal development of the endocranium. Similarly to the ectocranial counterpart, the endocranium shows a variable position of the maximum width when different groups among the genus *Homo* are compared. It is localized at the temporal lobes in the less encephalized taxa (*H. erectus s.l.*), at the lower parietal areas among the Neandertals (Bruner et al., 2003a), and at the upper parietal areas in modern humans (Holloway, 1981a; Grimaud-Hervé, 1997). Although the vault of CPR is deformed by the diagenetic processes, CPR clearly shows the first and less derived morphology.

The available information on the cerebral asymmetries and petalias in CPR is difficult to interpret in terms of evolution and variation, given the poor knowledge regarding this feature in extinct *taxa* and even in extant human populations (e.g. Le May, 1976; Holloway and De La Coste-Lareymondie, 1982; Grimaud-Hervé, 1997; Bruner et al., 2003b).

The flattening of the occipital lobes in CPR (i.e., rather compressed onto the parietal-temporal region) has to be considered another plesiomorphic retention shared with early *Homo* representatives, whereas a diverse and de-

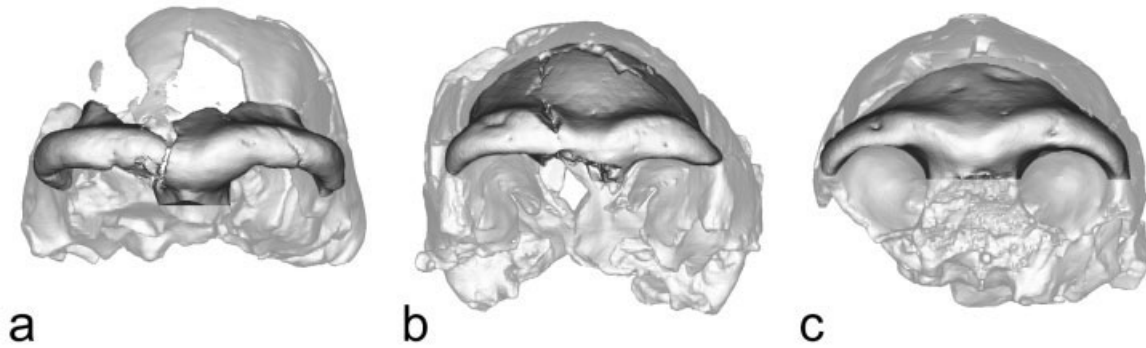


Fig. 12. Digital replicas of OH9 (a), Ceprano (b), and Bodo (c) in frontal view (the facial volumes of Bodo have not been included). The supraorbital structures are evidenced.



Fig. 13. Midsagittal sections from the digital replicas of OH9 (a), Bodo (b), Ceprano (c), and midsagittal tomographic slice of Kabwe (d).

rived status in the Asian *H. erectus* hypodigm may be inferred. The occipital lobes are localized posteriorly to the parietal-temporal complex and more projecting in weakly encephalized morphotypes (Holloway, 1981b; Bruner, 2003). This morphology has been claimed to be a plesiomorphic retention from early *Homo* (Grimaud-Hervé, 1997). Alternatively, this morphology has been hypothesized to be restricted only to *H. erectus* (sensu stricto), since it is missing in African Middle Pleistocene endocasts

(i.e. Salé; Bruner, 2004) or even in more ancient crania such as in the 1-million-year specimen from Buia (E.B., personal observation).

The morphology of the confluence of sinuses and the larger left sigmoid sinus apparently suggests the dominance of the right parieto-occipital hemisphere, despite the fragmentation of the posterior regions of the cranial vault, which does not allow one to assess this interpretation firmly. When the phenotypic plasticity of the vascular

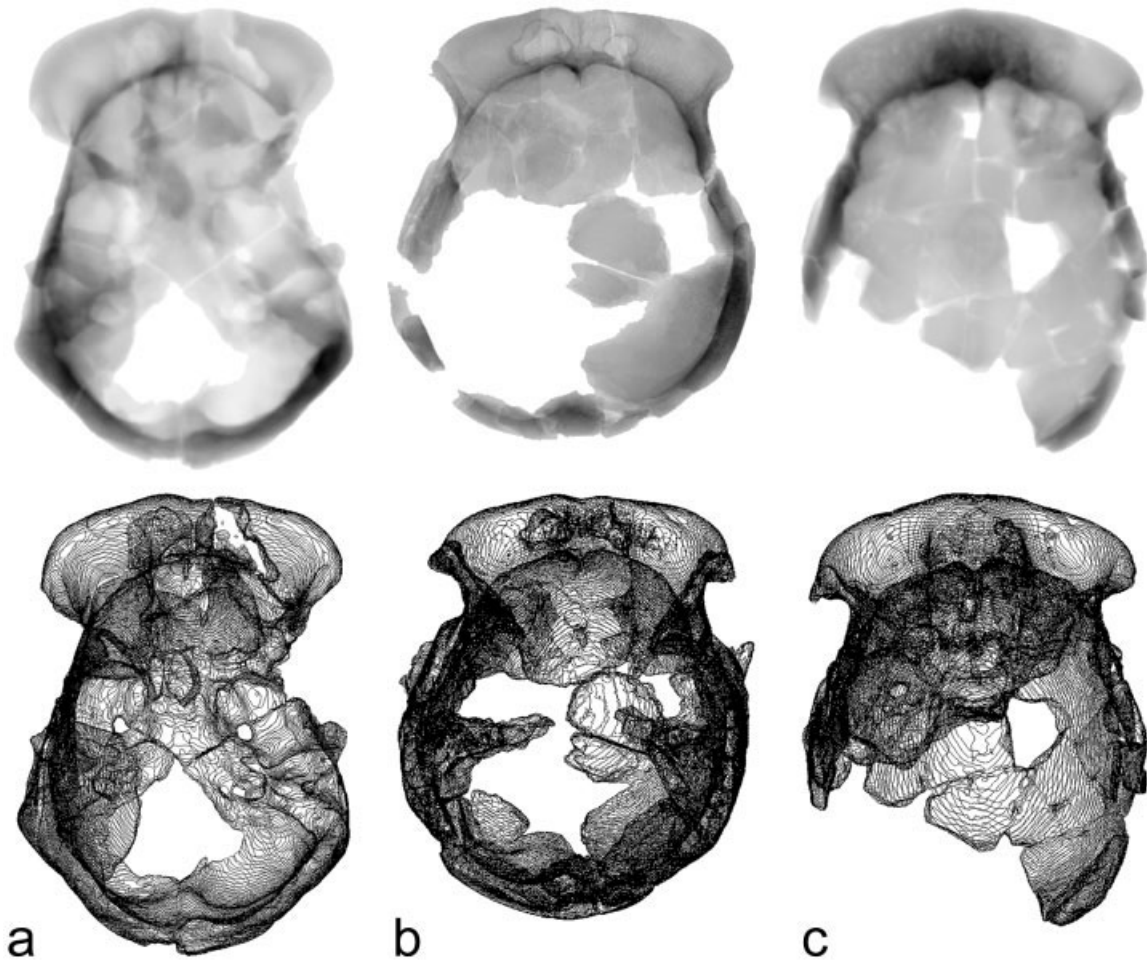


Fig. 14. Dorsal view of the OH9 (a), Ceprano (b), and Bodo (c) neurocrania, by polyline interpolation (below), and respective scout views through sum of gray values (above).

endocranial system (Mannu, 1911; Romagna-Manoia, 1911; Kimbel, 1984; O’Laughlin, 1996) and the independence of the inner and outer bone surfaces (Moss and Young, 1960) are considered, it can be suggested that an extended right occipital lobe will involve a stronger pressure on the inner table, promoting the blood outflow on the jugular system of the opposite side and its vascular development.

The traces of the middle meningeal system are far from being understood, in part because of limited knowledge of vascular dynamics (Marcozzi, 1942; Falk and Nicholls, 1992; Falk, 1993) and variability (see Grimaud-Hervé, 1997; Bruner, 2003; Bruner et al., 2003b). The platycephalic condition and the occipital projection described for skulls from Sangiran, Trinil, and Zhoukoudian are associated with a larger prevalence of posterior dominance of the middle meningeal system, where a parietal (obelic) ramus is considerably developed and splits from the posterior branch of the main path (Grimaud-Hervé, 1994, 1997). In contrast, modern humans and Neandertals show a more developed anterior system. CPR displays a pattern that appears similar to these second morphotypes. It should be tested whether or not the morphology of the

middle meningeal vessels is related to structural constraints and to the overall endocranial size and shape. In this case, the morphology of the meningeal vessels described in CPR could be a secondary consequence of the vertical development associated to the relative a-p shortening of the occipital areas.

Place of Ceprano in Human Evolution

For a long time, the hard evidence for human evolution between 1.6 and 0.6 Myr BP was noticeably scarce (e.g., Rightmire, 1990), including the incomplete calvarium from Olduvai (OH9) and many other more fragmentary specimens from southeastern Africa, the mandibles from Ternifine in north Africa, part of the poorly dated fossil record from both the island of Java (sites of the Pucangan formation) and China (e.g., Gongwangling). Thus, excluding the Far Eastern fossil record, the earliest presence of humans in most regions of Eurasia was inferred only from archeological assemblages referred to the Oldowan (or “mode 1”; Clark, 1968) and/or Acheulean (“mode 2”) technotypes of the Lower Paleolithic, whose succession in Europe (e.g., Peretto, 2001) and Near East (e.g., Goren-Inbar et al., 2000) postdates at least 0.5 Myr the chronol-

ogy of the analogous Paleolithic transition recorded in Africa (Asfaw et al., 1992).

Recently, new findings have enlarged the available evidence in east Africa, with fossils like those discovered at Buia (Abbate et al., 1998), Bouri (Asfaw et al., 2002), and Olororgesailie (Potts et al., 2004) starting to fill the gap. Together with the extensive fragmentary material from Atapuerca-TD6 (Carbonell et al., 1999), CPR represents the European counterpart of these African fossil findings. Thus, a comprehensive knowledge of its morphology is required to understand the evolutionary processes ranging around 1 Myr BP (e.g., Manzi, 2004).

As already mentioned in the introduction, a systematic consideration of the CPR affinities based on a set of ectocranial traits suggested independence from *H. erectus s.l.* (Ascenzi et al., 2000; Manzi et al., 2001a), differently from previous claims (Ascenzi et al., 1996; Clarke, 2000). At the same time, the set of apomorphies shared with *H. heidelbergensis* were demonstrated to be largely incomplete, preventing a possible attribution to this *taxon*. As a conclusion, the interpretation of CPR as a morphological bridge between *H. erectus s.l.* and the Afro-European Middle Pleistocene variability was suggested (Manzi et al., 2001a; Manzi, 2004).

Even from the present study, a number of features in the Ceprano calvarium seem to represent plesiomorphic traits shared with early *Homo* taxa, involving a general archaic morphology of the specimen. In contrast, the presence of some derived anatomical traits suggests a phenotypic relationship with populations referred to the subsequent and polymorphic species *H. heidelbergensis* (sensu Rightmire, 1998). These considerations allow us to make inferences about the phylogenetic significance of CPR for human evolution, especially when its chronology and topology are considered.

By contrast, this intermediate position between definitely archaic and more derived morphotypes of the genus *Homo* is not found in the calvarium coming from the Dakanihylo Member of the Bouri Formation, Middle Awash, whose affinities may be more closely found within the African *H. erectus* (or *H. ergaster*) range of variation (Manzi et al., 2003; Manzi, 2004; but compare Gilbert et al., 2003). It seems that similar phenetic considerations might also be appropriate for both the penecontemporaneous and partly described cranium from Buia (Abbate et al., 1998) and the largely incomplete specimen from Olororgesailie (Potts et al., 2004). It thus seems that the ancestral phenotype to the variability observed among the populations of the Middle Pleistocene in Africa and Europe has to be searched for outside the sub-Saharan African regions. At present, CPR represents the best available candidate for such a position in human evolution, while in eastern Asia the maintenance of features referable to *H. erectus* (sensu stricto) is observed for a long time.

Such a scenario appears supported further by our present analysis. However, a taxonomic attribution for the Italian specimen remains puzzling. A direct comparison between CPR and the sample from Atapuerca-TD6 is not feasible so far, but for a few traits (as reported by Manzi, 2004). Nonetheless, we have no reason at present to exclude CPR from the range of variation of the still hypothetical species *H. antecessor* (Bermúdez de Castro et al., 1997; Arsuaga et al., 1999), particularly when this *taxon* is viewed as a widespread morphotype that was ancestral to the human lineage(s) of the Middle Pleistocene.

ACKNOWLEDGMENTS

The authors thank the Soprintendenza Archeologica del Lazio for authorizing and supervising researches on the Ceprano calvarium as well as excavations in the Ceprano-Campogrande area. The CT scan was carried out at the Hospital Pio XI in Rome in virtue of the generous hospitality and cooperative assistance of Dr. Gianfranco Gualdi and his staff (with a special mention to S. Caprasecca). Marie-Antoinette and Henry de Lumley kindly allowed the analysis of the endocast collection preserved at the Institute de Paléontologie Humaine (Paris), while Juan Luis Arsuaga permitted the evaluation of endocasts at the human evolution laboratories of the Universidad Complutense (Madrid); Dominique Grimaud-Hervé, Ana Gracia, Patricio Dominguez, and Carlos Lorenzo provided invaluable assistance. The authors also express their gratitude to Chris B. Stringer and Fred Spoor, who kindly furnished CT images and information about the fossil specimens from Kabwe and Petralona. They are also grateful to a number of people for suggestions, criticisms, and assistance, especially to Aldo and Eugenia Segre, Italo Biddittu, Simone Mantini, and Pietro Passarello. Jeff Laitman and two referees improved this article with constructive comments and suggestions.

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