

A cranium for the earliest Europeans: Phylogenetic position of the hominid from Ceprano, Italy

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The human fossil evidence unequivocally pertaining to the first inhabitants of Europe at present includes the sample from Atapuerca-TD6 (Spain) and the incomplete adult calvaria discovered near Ceprano, in Southern Latium (Italy). On the basis of regional correlations and a series of absolute dates, the age of the Ceprano hominid is estimated to range between 800 and 900 kilo-annum (ka). In addition, the association with archaic (Mode 1) Paleolithic findings from the same area is suggested. After the completed reconstruction of the calvaria, we present here a new study dealing with the general and more detailed aspects of the morphology displayed by Ceprano, in comparison to fossil samples ranging between Early and Middle Pleistocene. According to our results, cranial features indicate that Ceprano represents a unique morphological bridge between the clade *Homo ergaster/erectus* and later Middle Pleistocene specimens commonly referred to *Homo heidelbergensis* (and/or to *Homo rhodesiensis*), particularly those belonging to the African fossil record that ultimately relates to the origin of modern humans. In conclusion, given its geographical, chronological, and phylogenetic position, an attribution to the species *Homo antecessor* is considered, although the sample from Atapuerca-TD6 is not directly comparable to Ceprano. Alternatively, a new species—ancestral to later European and African hominines—should be named to accommodate such a unique fossil specimen.

The presence of human populations in Europe before the 500-ka age range indicated by advocates of the so-called "short chronology" (1) has been claimed for a long time on the basis of archaeological discoveries in various corners of the continent. Examples of pre-500-ka localities are Le Vallonet, in France (2), Monte Poggiolo, in Italy (3), and those in the Guadix-Baza Basin, Spain (4). In 1994, unequivocal human fossil evidence pertaining to the time range at the boundary between Early and Middle Pleistocene was found in the sites of Atapuerca Gran Dolina (Spain; ref. 5), including a sample of fragmentary juvenile specimens and dental remains, and Ceprano (Italy; ref. 6), where an incomplete adult calvaria was discovered. Roughly one million years earlier, hominids are present at the "gates of Europe," in Georgia (7). It is, however, to be demonstrated that early *Homo* diffused in Europe at that time, whereas an occupation of East Asia can be inferred (8–10).

Acheulean assemblages are widely diffused in Europe from about 600 ka (11) and fossil human remains are also present in various sites, such as at Mauer, Arago, Bilzingsleben, Vértesszöllös, Visogliano, and so on. According to the scenario indicated by some authors during the last decade (12, 13), these ancient Europeans can be referred to *Homo heidelbergensis*, a paleospecies that (according to the same point of view) also includes a large part of the Middle Pleistocene African fossil record, represented by specimens such as Bodo, Kabwe, and others. At the same time, the more traditional notion of a single multiregional Middle Pleistocene phase—the so-called "archaic *Homo sapiens*"—have been abandoned by the majority of the authors. Alternatively, in the presence of a stem species named *Homo antecessor* (14), another scenario has to be considered in which

the European and African clades are distinguished as separate morphotypes, respectively referable (if distinguished at the species level) to *H. heidelbergensis* and to *Homo rhodesiensis*. Concurrently, human populations from this general time span in the Far East are mostly regarded as representatives of another regional clade, the species *Homo erectus* (15, 16).

Given these alternative scenarios, the discovery and/or re-evaluation of fossil specimens that may fill the chronological gap between the most ancient African evidence pertaining to the genus *Homo* and subsequent biogeographical human radiation in the Early and Middle Pleistocene is of critical importance. From this perspective, the recently discovered crania and mandible from Dmanisi, dated to about 1.7 mega-annum (Ma) (see ref. 7), can be regarded as the evidence of one of the earliest, if not the earliest, human diffusions out of Africa. Yet, the time span between 1.5 and 0.5 Ma still remains relatively poor in terms of human fossil evidence. In the late Early Pleistocene, in particular, there are very few well preserved fossils in Africa (17) or in Eurasia (see, e.g., ref. 13). Among them, the Ceprano calvaria occupies a crucial position, as far as its chronology and morphological features are concerned. In this framework, the present paper provides a comparative analysis of this fossil, based on a new reconstruction (18, 19). This study is aimed at evaluating the significance of the Italian specimen for the evolution of the genus *Homo*.

Dating and General Features of Ceprano. The circumstances of recovery of the fossil hominid by I. Biddittu at Campogrande near Ceprano, the geostratigraphy, the chronology, and the archaeology of the site have been described (see refs. 6 and 19–21). In brief, according to the interpretation given by Ascenzi and coworkers on the basis of regional correlations synthesized in Fig. 1, the cranium should be referred to the time span between the Acheulean site of Fontana Ranuccio [about 458 ka (22)] and layers with volcaniclasts dated by ⁴⁰Ar/³⁹Ar to around 1 Ma (23, 24). In addition, given the absence in the sediments containing the cranium of any leucitic remnants of the more recent volcanic activity known in the region—that are referred to the range between 100 and 700 ka (25)—and the presence above the cranium itself of a clear stratigraphic unconformity that marks the lowest limit of the sandy leucitic pyroclasts, an age between 800 and 900 ka is at present our best chronological estimate.

As a consequence of the age estimate, a possible association of the hominid from Ceprano with pebble/flakes (i.e., Mode 1) assemblages in the same region (Southern Latium)—from sites such as Castro dei Volsci, Arce, and Fontana Liri (26)—has been suggested.

The current form of the Ceprano calvaria (Fig. 2) is the result

Abbreviations: ka, kilo-annum (thousand years ago); Ma, mega-annum (million years ago); NJ, neighbor-joining; UPGMA, unweighted pair group method using arithmetic averages.

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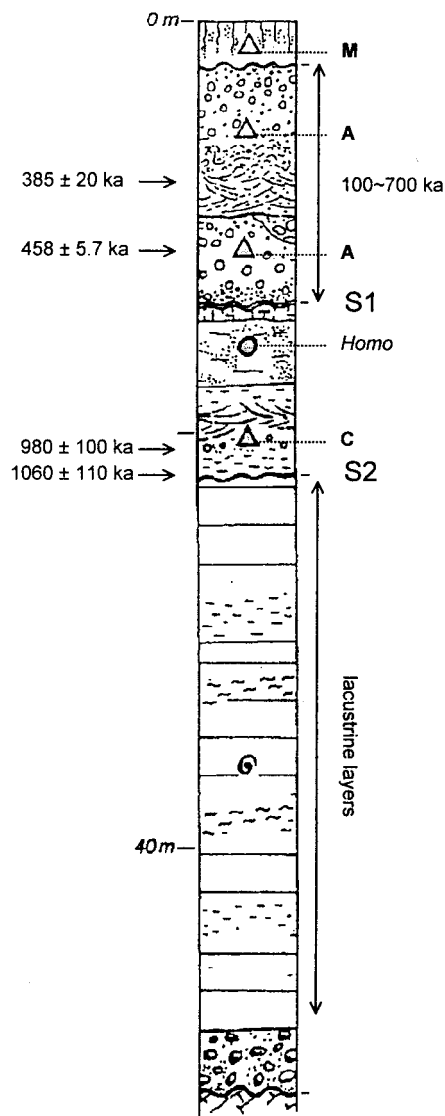


Fig. 1. Simplified stratigraphic sequence of the central Ceprano Basin composed by A. G. Segre from various test sections in the region (redrawn from ref. 17; see text for other references). The position of the human cranium is marked with a circle, whereas triangles indicate archaeological layers: M, Mousterian; A, Acheulean; C, "archaic" Paleolithic. In relationship with two major unconformities in the sequence, S1 and S2, indicate the lowest limits of sands with leucitic pyroclasts (younger volcanic activity; referred to the range between 100 and 700 ka) or without leucitic pyroclasts (volcanic activity older than 700 ka), respectively. Available K-Ar datings in the region are also reported on the left.

of a process started in 1994 and concluded in 1999. It is based on the original reconstruction by Ascenzi and coworkers (see ref. 6), subsequently corrected by R. J. Clarke (18) and further revised by M. A. de Lumley and F.M. (19). Looking at the cranium along its transversal contour, Ceprano is presently constituted as follows. On the right side the virtually complete frontal bone articulates in two points with fragments of the parietal along the coronal suture and also with the greater wing of the sphenoid, which also articulates with the temporal squama (endocranial surface). The right parietal—well represented, particularly in its posterior component—articulates with both the temporal and the largely preserved occipital bone along the preserved segments of the lambdoid suture. Both the right and left mastoid portions of the temporal bones articulate with the

occipital in the asterionic regions and for part of the occipito-mastoid suture. On the left, the squama of the temporal bone is in connection with few residual fragments of the parietal and with the preserved part of the sphenoid; the latter, in turn, is connected with the frontal. Thus, cranial shape can be confidently examined, because all of the preserved cranial portions connect directly with each other.

The cranial vault of Ceprano is low and gently curved along the midsagittal profile; the maximum length is between glabella and inion, which is therefore coincident with the opistocranium. At the same time, however, the cranium is relatively short, with considerable transversal expansion. As a result, Ceprano is brachicranic, an unusual trait in archaic *Homo*. The maximum breadth is at the level of the supramastoid crests.

A massive and continuous torus with supratoral sulcus characterizes the receding squama of the frontal bone. In the supraorbital region we observe an interesting suite of traits. The glabella area is depressed in both superior and frontal views; on both sides, the torus shows a variable thickness, growing steeply from the midsagittal plane, reaching maximum height around midline of each orbit, and gradually decreasing laterally. We also observe torsion of the superficial aspect of the supraorbital ridges, with a flat and vermiculate medial component clearly distinguishable from the more rounded and bulging lateral part. By contrast, the superior border of the orbits is almost rectilinear. The interorbital width is great, and frontal sinuses extend laterally and posteriorly. The cranium exhibits moderate post-orbital constriction and marked temporal lines on both the frontal and (right) parietal bones. There are no indications of frontal, coronal, or parietal keelings, although a slight parabregmatic depression is visible. The parietal (right side) is square in shape, relatively flattened sagittally, and markedly angled in coronal sections at the level of the temporal lines. The superior border of the temporal squama is missing, but it can be hypothesized that it was relatively high and curved. The mandibular fossa (incompletely preserved) is relatively small and deep, and is bordered by a prominent entoglenoid process. The tympanic bones are bilaterally lost, and the mastoid processes are massive. The occipital squama is wide and flat; in lateral view, the occipital is angled, characterized by the presence of transverse occipital torus with supratoral sulcus. Inion and endinion are clearly separated. The torus does not reach the asterionic region on both sides, thus it is not continuous with the well defined angular torus or with the supramastoid crests. The nuchal plane is preserved only in part, and large areas of the cranial base are unfortunately missing or damaged. Thickness of the bones of the cranial vault is exceptional, reaching values above 20 mm (temporal asterion).

Metric data recorded on the new reconstruction of the Ceprano calvaria have recently been published in detail (19). The selection of bivariate metric comparisons shown in Fig. 3 demonstrates that Ceprano fits within the variability of archaic *Homo* and is frequently associated with the more massive specimens in that sample, such as Sangiran 17, Petralona, and the Cranium 4 from Sima de los Huesos. One of the most peculiar traits of Ceprano is confirmed to be the relatively large breadth, especially compared with its maximum length, as clearly demonstrated by the diagram in Fig. 3a. The considerable value of frontal expansion (Fig. 3b) is closer to European specimens of the Middle Pleistocene generally referred to *H. heidelbergensis*. However, the distance between glabella and inion (Fig. 3a), as well as the relationship between frontal and parietal midsagittal chords (Fig. 3c), relate Ceprano with fossils from Zhoukoudian and give the Italian specimens a resemblance to *H. erectus* and/or to *Homo ergaster* in lateral profile. In addition, the proportions of the occipital bone reported in Fig. 3d indicate that Ceprano has a wide upper scale, proportionally high (lambda-inion chord) and large (biasterionic breadth), leading to a position in the plot close to that of ER-3733.

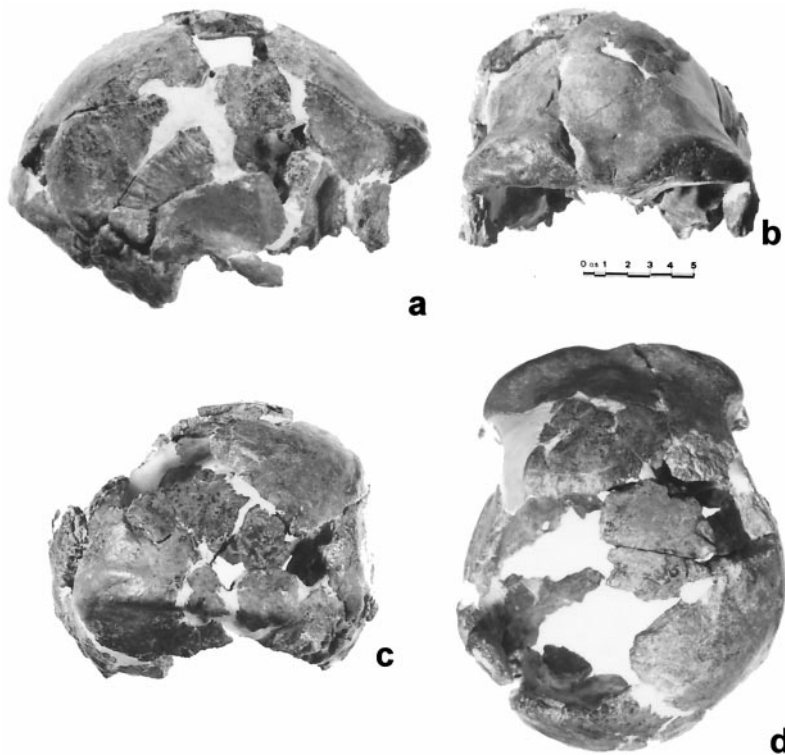


Fig. 2. The new reconstruction of the Ceprano calvaria in four views: (a) right lateral; (b) frontal; (c) occipital; (d) superior.

Discrete Traits: A Multivariate Comparative Analysis. From this overview of the general features displayed by Ceprano, the original preliminary attribution to *H. erectus* (ref. 6; see also ref. 18) does not appear completely satisfactory, and should be reconsidered. As a matter of fact, the variability of this taxon appears surprisingly extensive when the Italian specimen is included in the hypodigm. As we already stated elsewhere (19): “to assess its affinities to *H. erectus* additional comparisons will need to be made with other taxa, particularly *H. heidelbergensis* and *H. antecessor*.”

To shed some light on the phylogenetic and taxonomic position of Ceprano, thirty character states have been examined in a series of 20 specimens ranging between Early and Middle Pleistocene, sufficiently complete to be compared with the calvaria from Ceprano. Selection of traits derives from lists of distinctive features generally considered in describing *H. erectus* and related hominines [see table 2.11 in Wood (27)]. Given the peculiar character of the frontal region in Ceprano, special attention has been devoted to features describing the supra-orbital structures. The traits that have been considered and

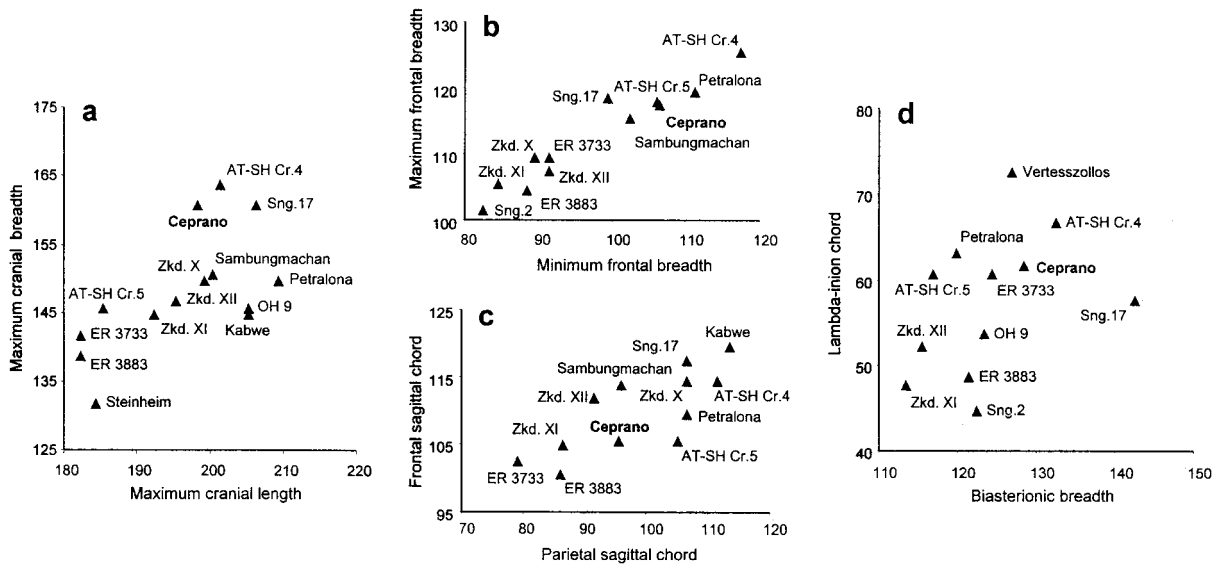


Fig. 3. Bivariate morphometric comparisons between Ceprano and archaic *Homo* samples. (a) maximum cranial length vs. maximum cranial breadth; (b) minimum frontal breadth (Martin measurement n. 9) vs. maximum frontal breadth (n. 10); (c) parietal sagittal chord (from bregma to lambda) vs. frontal sagittal chord (from nasion to bregma); (d) biasterionic breadth vs. lambda-inion chord. A more extensive collection of measurements obtained on the new reconstruction of the Ceprano calvaria is reported in ref. 16. Site/specimen abbreviations are as in Table 1.

Table 1. Alternative character states in Ceprano and comparative samples

	Africa						Asia						Europe							
	ER 3733	ER 3883	OH 9	Bodo	Kabwe	Saldanha	Dmn. 2280	Dmn. 2282	Sng. 2	Sng. 17	Zkd. III	Zkd. X	Zkd. XI	Zkd. XII	Ceprano	Arago	Steinheim	Petalona	At-SH Cr.4	At-SH Cr.5
Long cranial vault	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1
Low cranial vault	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Maximum breadth across the angular torus or supramastoid crest	1	1	1	—	1	—	1	1	1	1	1	1	1	1	1	—	0	1	1	1
Thick vault bones (parietal)	0	1	1	1	0	1	1	—	1	1	1	1	1	0	1	0	0	0	1	1
Pronounced postorbital constriction	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Frontal keel or ridge	1	0	0	0	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0
Straight junction of torus and frontal squama	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1
Coronal ridge	1	1	—	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Flattened parietal	1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0
Rectangular parietal	0	0	0	—	1	1	1	1	0	1	0	1	0	0	0	0	0	1	1	0
Low temporal squama	0	1	1	0	0	—	1	1	1	1	1	1	1	1	0	—	0	0	0	0
Flat superior border of the temporal squama	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	—	0	0	0	0
Small mastoid process	1	0	1	—	0	—	1	1	1	1	1	1	1	1	0	—	1	0	0	0
Opisthocranion coincident with inion	1	1	1	—	0	1	1	1	1	1	1	1	1	1	1	—	0	1	0	0
Sharply angulated occipital profile	1	0	1	—	0	1	1	0	1	1	1	1	1	1	1	—	0	0	0	0
Broad nasal bones	0	0	1	1	1	—	0	—	—	1	1	1	1	1	1	1	1	1	1	1
Horizontal inferior border of the supraorbital torus	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0
Continuous thickness of the supraorbital torus	1	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1
Glabellar inflexion in superior view	1	1	1	1	1	1	0	—	—	0	1	0	0	0	1	1	1	1	1	1
Ceprano-like “torsion” of the supraorbital torus	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0
Bilateral discontinuity (ridges) of the supratatorial sulcus	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0
Prominent angular torus at mastoid angle	0	0	1	—	0	0	1	1	0	0	1	1	1	1	1	1	0	1	1	1
Marked supramastoid crests	1	1	0	—	1	—	1	1	1	1	1	1	1	1	1	—	0	1	1	1
Marked mastoid crests	1	0	1	—	1	—	1	1	0	0	1	1	1	0	0	—	0	—	1	1
Occipitomastoid ridge	0	0	0	—	1	—	—	—	1	1	1	1	1	1	1	—	1	—	1	1
Juxtamastoid ridge absent	0	1	0	—	1	—	—	—	1	1	1	1	1	1	1	—	0	—	1	1
Suprameatal tegmen	1	0	1	—	1	—	1	1	1	1	1	1	1	1	1	—	0	1	0	0
Occipital torus with supratatorial sulcus	0	0	0	—	1	0	0	0	1	0	1	1	1	1	1	—	0	1	1	1
Occipital torus continuous with angular torus and supramastoid crest	0	0	0	—	1	1	0	0	1	1	1	0	0	0	0	—	0	0	1	0
Mid-sagittal depression of the occipital torus	0	0	0	—	—	0	0	0	0	0	0	0	0	0	0	—	1	0	1	1

0/1 = absent/present. Site/specimen abbreviations: At-SH = Atapuerca Sima de los Huesos; Dmn. = Dmanisi; ER = East Turkana; Ngd. = Ngandong; OH = Olduvai; Sng. = Sangiran; Zkd. = Zhoukoudian.

specimens that have been examined are listed in Table 1, where the scores for presence or absence are also reported.

From these data, a matrix of Manhattan phenetic distances was calculated (Table 2). These distances have been used to generate unrooted trees respectively based on neighbor-joining (NJ) and unweighted pair group method using arithmetic averages (UPGMA; 28, 29); both these trees are reported in Fig. 4. Consistent results were also obtained when applying multivariate analyses to raw discrete data, but with the limitation that several rows or, alternatively, columns had to be excluded because of missing scores.

In general, the distribution of the specimens in the trees appears consistent with the assumption that specimens with obvious affinities—like those coming from the same site (i.e., Dmanisi, Zhoukoudian, and Sima de los Huesos)—should cluster together as they actually do. Given this consistency with the expectations and merging the results reported in both the NJ-based and UPGMA-based trees with the *H. erectus* architectural resemblance of the Ceprano calvaria (see above), the position of the late Early Pleistocene Italian specimen appears of great interest for our knowledge on the relationships between populations/species of the genus *Homo*.

Two main clusters are evident in Fig. 4 (a and b). Differences between the trees appear minimal and only concern the relative

position of a few specimens. Particularly, Ceprano in the NJ-based tree stands in an isolate position (Fig. 4a), whereas in the UPGMA-based tree is grouped with the African Middle Pleistocene sample (Fig. 4b).

A first main cluster in both the trees includes the Asian specimens from Sangiran and Zhoukoudian, generally referred to *H. erectus (sensu stricto)*, with the possible inclusion of the African OH-9. Another association of this same cluster includes fossils from both Turkana and Dmanisi. In this light, the two Georgian crania appear appropriately classified as *H. ergaster* (according to ref. 7). A second cluster describes a completely separate area of the two graphs, as it groups Middle Pleistocene specimens from Africa and Europe that find in Ceprano a plausible ancestral morph. Consistent with its morphometric features (Fig. 3), in fact, Ceprano appears in the trees—particularly looking at the NJ analysis (Fig. 4a)—as a morphological “bridge” between the *H. ergaster/erectus* group and that composed by specimens commonly referred to *H. heidelbergensis*. In addition, the difference observed when using UPGMA to generate the tree (Fig. 4b) is the more close clustering of the European Ceprano with the African Middle Pleistocene specimens: Bodo, Kabwe, and Saldanha. However, looking at both the trees, it should be borne in mind the general (architectural) resemblance in shape between Ceprano and fossils ascribed to *H.*

Table 2. Matrix of phenetic distances based on data in Table 1

	ER 3733	ER 3883	OH 9	Bodo	Kabwe	Saldanha	Dmn. 2280	Dmn. 2282	Sng. 2	Sng. 17	Zkd. III	Zkd. X	Zkd. XI	Zkd. XII	Ceprano	Arago	Steinheim	Petralona	At-SH Cr.4	At-SH Cr.5	
ER 3733	0.000																				
ER 3883	0.333	0.000																			
OH 9	0.276	0.345	0.000																		
Bodo	0.688	0.625	0.533	0.000																	
Kabwe	0.517	0.586	0.714	0.250	0.000																
Saldanha	0.524	0.476	0.550	0.071	0.300	0.000															
Dmn. 2280	0.286	0.464	0.370	0.563	0.481	0.381	0.000														
Dmn. 2282	0.280	0.360	0.292	0.538	0.458	0.421	0.120	0.000													
Sng. 2	0.393	0.321	0.296	0.571	0.556	0.500	0.385	0.440	0.000												
Sng. 17	0.367	0.367	0.310	0.688	0.552	0.524	0.321	0.360	0.143	0.000											
Zkd. III	0.333	0.333	0.276	0.688	0.517	0.571	0.357	0.360	0.143	0.167	0.000										
Zkd. X	0.367	0.433	0.241	0.688	0.552	0.667	0.250	0.280	0.214	0.133	0.167	0.000									
Zkd. XI	0.333	0.400	0.207	0.688	0.586	0.714	0.286	0.320	0.179	0.167	0.133	0.033	0.000								
Zkd. XII	0.333	0.400	0.276	0.750	0.586	0.762	0.357	0.360	0.179	0.167	0.133	0.100	0.067	0.000							
Ceprano	0.533	0.533	0.448	0.188	0.448	0.381	0.500	0.440	0.429	0.500	0.400	0.433	0.400	0.400	0.000						
Arago	0.438	0.500	0.333	0.357	0.438	0.400	0.625	0.385	0.571	0.625	0.375	0.563	0.500	0.438	0.250	0.000					
Steinheim	0.433	0.500	0.483	0.375	0.517	0.476	0.714	0.560	0.607	0.600	0.567	0.667	0.633	0.567	0.500	0.125	0.000				
Petralona	0.444	0.444	0.500	0.250	0.269	0.333	0.519	0.417	0.520	0.593	0.481	0.519	0.481	0.481	0.333	0.250	0.407	0.000			
At-SH Cr.4	0.600	0.467	0.586	0.375	0.345	0.476	0.643	0.520	0.571	0.567	0.467	0.500	0.533	0.600	0.400	0.375	0.433	0.296	0.000		
At-SH Cr.5	0.533	0.400	0.517	0.250	0.345	0.476	0.571	0.520	0.500	0.633	0.467	0.500	0.467	0.533	0.400	0.313	0.367	0.222	0.133	0.000	

ergaster and/or to *H. erectus* (see above)—a feature, actually a suite of features, that is not included in these analyses.

Affinities between Ceprano and Middle Pleistocene specimens from Africa and Europe include: absence of pronounced postorbital constriction, absence of clear keeling or ridges on the vault (with the exception of Kabwe), higher and more rounded temporal squama than in *H. erectus*, relatively large mastoids (with the exception of Steinheim), and features of the supraorbital torus (such as the presence of a labellar inflexion). Some

frontal features in particular—namely the discontinuous thickness of the torus, marked by a definite midorbit torsion (see above)—indicate a relationship between Ceprano and the Middle Pleistocene fossil record from Africa closer than with the Anteneandertal European specimens (as evidenced by the UPGMA-based tree).

Interestingly, therefore, Ceprano appears as the most archaic—for the “*erectus*-like” parieto-occipital vault—and the most ancient specimen to display this kind of morphology in the

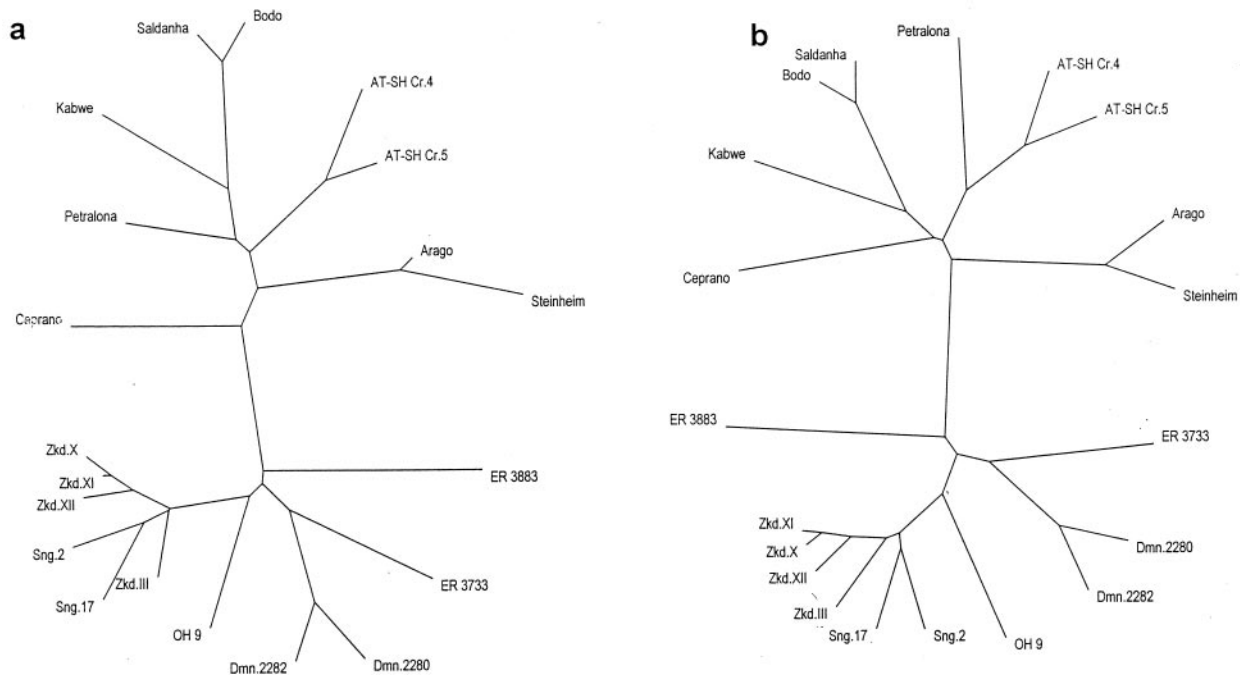


Fig. 4. NJ (a) and UPGMA (b) unrooted trees (28, 29) derived from weighted Manhattan distances reported in Table 2. Site/specimen abbreviations are as in Table 1.

frontal region. Unfortunately, little can be said about the face (with a few exceptions, such as the relative dimension of the nasal bones). Taken as a whole, its morphological pattern is diverse from that shared by *H. ergaster* and *H. erectus*. Given the dating of the Italian specimen, it is also new with respect to later *Homo* referred to *H. heidelbergensis* (and to *H. rhodesiensis*; if a distinction at the species level of the African group is preferred). 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 Neandertals and modern humans.

Conclusions: Toward an Interpretation. On the basis of these results and evaluations, we suggest that humans represented by Ceprano—bearing a new morphology and clear signs of greater encephalization (demonstrated, e.g., by the frontal proportions; see Fig. 2*b*)—diffused into the northern hemisphere during the late Early Pleistocene, in association with Mode 1 Paleolithic technologies. According to the evidence furnished by Ceprano, part of this new morphology was subsequently lost during human evolution in Europe as a possible consequence of the arrival of Acheulean immigrants, whose presence seems to be widely attested in the continent only after 600 ka. At the same time, it should be concluded that this phenotype further developed in Africa during the Middle Pleistocene, as indicated by the affinities between Ceprano and specimens like Bodo or Kabwe.

Which species is then represented by Ceprano? Given its geographical, chronological, and possible phylogenetic position (as described above), the best comparison should be represented by the fossil sample unearthed from Gran Dolina (level TD6) at

Atapuerca (Spain). Unfortunately, among the nearly 80 fossil pieces that have been found so far at that site, and referred to the species *H. antecessor* (5, 14, 30), none is directly or adequately comparable with Ceprano, at least in terms of completeness (as for some temporal bone fragments) or age at death (as in the case of the juvenile frontal TD6-15). It is not possible at present to predict the morphologies that could be discovered at Atapuerca, when level TD6 will be reached again by future excavations. However, we cannot exclude that affinities will emerge with what we observe now on Ceprano; in this case, this calvaria would describe for the first time the adult cranial morphology of *H. antecessor*. Alternatively, a less parsimonious scenario should be invoked, where two different human morphs were present during the same time span in Europe, and a new species should be named to accommodate the Italian specimen. Nevertheless, any scenario has to face with the fact that the Ceprano morphological pattern does not appropriately fit in the known ranges of variability of *H. ergaster/erectus*, from one side, and *H. heidelbergensis/rhodesiensis* from the other.

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