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C. R. Palevol 2 (2003) 153–159

COMPTES RENDUS
PALEVOL

Human Palaeontology and Prehistory / Paléontologie humaine et préhistoire

Homo cepranensis sp. nov. and the evolution of African-European Middle Pleistocene hominids

Francesco Mallegni [a,*], Emiliano Carnieri [a], Michelangelo Bisconti [b], Giandonato Tartarelli [c], Stefano Ricci [a], Italo Biddittu [d], Aldo Segre [d]

[a] *Archaeological Sciences Department, via S. Maria, 53, 56100 Pisa, Italy*
[b] *Earth Sciences Department, via S. Maria, 53, 56100 Pisa, Italy*
[c] *Scuola Normale Superiore, Piazza dei Cavalieri, 56100 Pisa, Italy*
[d] *Istituto Italiano di Paleontologia Umana, Piazza Mincio, 00100 Roma, Italy*

Received 4 November 2002; accepted 3 December 2002

(Dedicated to the memory of Professor Raffaelo Parente)

Presented by Yves Coppens

Abstract

The hominid calvarium from Ceprano (Italy) shows peculiar characters, especially in the frontal bone. This specimen differs from the other hominid species (*H. ergaster*, *H. erectus*, and *H. heidelbergensis*). The morphometric and the cladistic analyses show that the Italian fossil is a new hominid species. The typical characters of European *H. heidelbergensis* are absent in the frontal morphology of Ceprano, which is a representative of an African population that perhaps migrated at about 1.0 Ma (represented by the specimen from Bouri and as demonstrated by the cladistic analysis) and that did not ultimately contribute to the human population of Europe during the Middle and Late Pleistocene. On the other hand, Ceprano shares features with Middle Pleistocene *H. rhodesiensis*, and this allows us to suppose that Ceprano is an early relative of this African form. ***To cite this article: F. Mallegni et al., C. R. Palevol 2 (2003) 153–159.***

Résumé

***Homo cepranensis sp. nov.* et l'évolution des hominidés eurafricains du Pléistocène moyen.** Le crâne de Ceprano (Italie) montre quelques caractères anatomiques très intéressants, surtout en ce qui concerne l'anatomie de l'os frontal, qui diffère en cela de ceux des autres hominidés de l'hémisphère septentrional (*H. ergaster*, *H. erectus* et *H. heidelbergensis*). Les analyses morphométriques et cladistiques tendent à démontrer que le crâne de Ceprano peut représenter une espèce nouvelle. Les spécimens européens relatifs à *H. heidelbergensis* montrent des caractères différents et Ceprano peut être considéré, en Europe, comme le premier représentant d'une population d'origine africaine ; cette espèce émigra vers le nord il y a un million d'années environ (un autre représentant pourrait être Bouri, ainsi que l'analyse cladistique semble le démontrer). Il semble aussi que cette nouvelle espèce ne contribua que peu à l'établissement du peuplement humain des territoires septentrionaux pendant le Pléistocène moyen et supérieur. Ceprano semble annoncer, de par ces caractères, les formes humaines représentées par des

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* Correspondence and reprints.
E-mail address: mallegni@arch.unipi.it (F. Mallegni).

DOI: 10.1016/S1631-0683(03)00015-0

spécimens attribués à *Homo rhodesiensis* ; tout cela permet de supposer que Ceprano représente une forme précoce de ces derniers. ***Pour citer cet article : F. Mallegni et al., C. R. Palevol 2 (2003) 153–159.***

Keywords: Homo cepranensis; Middle Pleistocene; human evolution

Mots clés : Homo cepranensis ; Pléistocène moyen ; évolution des hominidés

1. Introduction

A hominid calvaria (Figs. 1–3) has been recovered in March 1994 and until today it can represent the most ancient fossil of Europe [1, 2]. It was very fragmented at the moment of the discovery but, several previous reconstructions [3, 7], one of the authors (F.M.) made the most complete one and satisfactory [4]. Because of the peculiar characters of this specimen, already described in a previous paper [16], we propose the creation of a new hominid species.

2. Description of *Homo cepranensis sp. nov.*

Order: Primates
Suborder: Anthropoidea
Superfamily: Hominoidea
Family: Hominidae
Genus: Homo
Species: *Homo cepranensis sp. nov.*

2.1. Etymology

The name comes from the site of provenance of this specimen, located in the Italian province of Frosinone (Latium), 90 km south of Rome.

2.2. Specific diagnosis

We propose a new hominid species featured by the following morphologies: cranial outline with low and short vault, showing evident bone thickness; opistocranion coinciding with the inion, maximum length comprised between glabella and inion, birsoid contour of the skull in superior norma; low, receding and relatively large frontal bone with a marked, almost continuous torus (browridge) and showing a slight depression close to the medial sagittal plane. The superciliary arches present an almost continuous arch up to the external supraorbital angle. The supratoral sulcus is almost continuous, while the specimen shows a bilateral fossa at the centre of the supraorbital arch, pro-

Fig. 1. Frontal view of Ceprano 1.
Fig. 1. Vue frontale de Ceprano 1.

Fig. 2. Lateral view of Ceprano 1.
Fig. 2. Vue latérale de Ceprano 1.

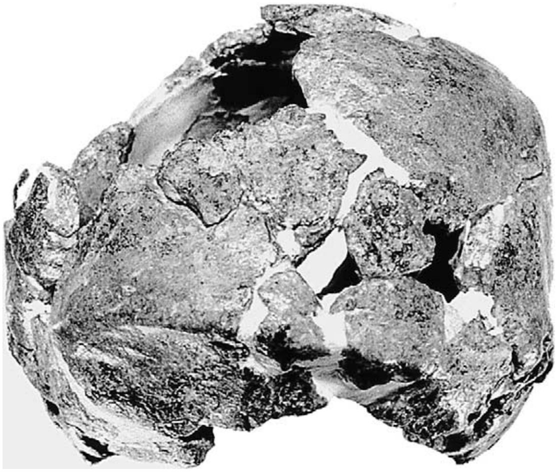

Fig. 3. Occipital view of Ceprano 1.
Fig. 3. Vue occipitale de Ceprano 1.

longing itself to the squama perpendicular to the torus, and almost to the supratoral sulcus superiorly. The starting of a separation between the superciliary and the orbital arch can be observed as a slight sagittal *lofus* up to the middle of the squama and an unmarked postorbital narrowing followed by almost parallel temporal lines. The parietal bones are quadrangular, the superior temporal lines are well marked: they end at the level of the torus angularis and are accompanied by a sulcus in their upper portion. The imprints of the middle meningeal arteries are very well marked. The maximum cranial breadth is measured between the *torus angularis* and the substantial supramastoid crest. On the contrary, the mastoid crests are fairly weak. The occipitomastoid crest ends at the asterion and there is no paramastoid crest; the suprameatal tegmen is quite well marked. The temporal squama develops with a sharply curved upper portion. The mastoid process has a large, pyramidal, attachment. The occipital bone is strongly angular and shows the *planum nuchae* larger than the *planum occipitale*. Endinion and inion do not coincide. The occipital torus is continuous and ends at the asterion with a slight supratoral sulcus. The cranial capacity has been calculated as 1180–1220 cc. The nasal bones had probably a large attachment at the level of the joint with the frontal bone.

2.3. Holotype

The holotype is Ceprano 1, a fragmented calvarium found by I. Bidittu on 13 March 1994. The specimen is housed in the Institute of Human Palaeontology, piazza Mincio 2, Rome, Italy (catalogue No. 944/1).

2.4. Site of discovery

Campo Grande of Ceprano, province of Frosinone, Italy. Geographic coordinates are: 13° 28' 50" longitude east – 41° 31' 40" latitude north.

2.5. Chronology

The specimen comes from a clay layer lying underneath a layer of volcanoclastic sands dated to 700 000 years BP by K-Ar.

2.6. Description of the calvaria, metrical and morphological comparisons

The specimen was collected in around 50 fragments, of which the largest was the frontal bone, followed by the right parietal, the two temporal bones and by part of the occipital squama. Fragments of the sphenoid bone and of the two frontal processes of the zygomatic bones were also recovered. The frontal bone has been restored and reconstructed from two parts, vertically separated at the beginning of the right torus. Orbital roofs are almost complete.

Part of the external compact bone (around 2 cm), running along the right coronal suture, has been lost. The left portion of the frontal bone lacks a trapezoid portion that starts just after the extreme part of the frontal torus and ends at the temporo-frontal suture. A few portions of the external compact bone around these larger portions are also missing.

We note two lesions on the external cranial surface, apparently resulting from perpendicular blows. One is visible at the midpoint of the right torus and another can be seen just above the left frontal prominence.

Two smaller, symmetrical lesions can be observed on the external upper margins of the frontal torus. The right parietal has been reconstructed from four fragments of which the central one is the largest. This bone is missing a sub-rectangular portion of the external compact bone, which corresponds to the loss observed on the frontal bone. The left parietal is almost absent (except a small portion just behind the coronal suture and another posterior portion, which is the angular torus).

The occipital bone is mainly preserved in its cerebral squama (of which a small portion is missing on the right), and is quite fragmented on its right side.

Both the temporal bones are almost complete, although the left one lacks a large portion of the external auditory meatus (this bone has been reconstructed from two fragments: squama and mastoid). The apices of the mastoid processes are eroded. The sphenoid bone has only its greater wings, and the right one is quite fragmented. The skull as a whole shows an evident deformation of its left side, caused by the burial conditions that put the occipital torus and the left cranial wall out of shape.

3. Comparison between *Homo cepranensis* and *Homo ssp* from Early and Middle Pleistocene

Based on the above considerations, we compare Ceprano with *H. ergaster, H. erectus* and *H. heidelbergensis* below.

Ceprano vs *H. ergaster* (KNM-ER-3733). Ceprano differs from *H. ergaster* in the following features: shorter cranial vault, thicker cranial bones, massive supraorbital torus, less pronounced postorbital constriction, occipital torus, with evident supratoral sulcus, higher endocranial capacity.

Ceprano vs *H. erectus* (Zou-khou-dian III, X, XI, XII, Sangiran 2, 17). Ceprano differs from *H. erectus* in the following features: shorter cranial vault, thicker cranial bones, double arch shaped supraorbital torus, less pronounced postorbital constriction, frontal keeling absent, coronal keeling absent, higher temporal squama, non flat margin of temporal squama mastoid processes stronger, varying thickness of the supraorbital torus laterally, 'torsion' of supraorbital torus, bilateral discontinuity of supratoral sulcus.

Ceprano vs *H. heidelbergensis* (Petralona, Arago, Steinheim, Saldanha, Kabwe). Ceprano differs from *H. heidelbergensis* in the following features: complex morphology of the frontal, especially in the toral area in which Ceprano shows a slight groove separating the supraciliar relief from the supratoral sulcus. Ceprano vs. *H. antecessor* (Gran Dolina level TD6). We think *H. antecessor* is not directly or adequately comparable with Ceprano, at least in terms of completeness or age at death [6].

4. Cladistic analysis

The phylogenetic relationships of *Homo cepranensis* were investigated through a cladistic analysis performed by the computer program PAUP 4.0b8a [19]. The goal of this study is to make explicit statements about the phylogenetic relationships of *Homo cepranensis* to the other previously named species of the genus *Homo* living during Early and Middle Pleistocene.

4.1. Methods

There are conflicting opinions about the use of cladistic analysis in the reconstruction of the human phylogeny [20]. However, it is clear that quantitative cladistics is useful when used to help solve the phylogenies of morphologically well-defined extinct species [8, 13, 14, 17]. For this reason, we have employed a quantitative cladistic approach in this work.

We analysed the following 20 skulls: ER3883, (*Homo ergaster*), DMN2280, DMN2282; OH9 (*Homo sp.*?), Bodo, Kabwe, Saldanha (*Homo rhodesiensis*), SNG2, SNG17, ZKD3, ZKD10, ZKD11 e ZKD12 (*Homo erectus*), Petralona, Arago, Steinheim, (*Homo heidelbergensis*) AT-SH-Cr4 and AT-SH-Cr5 (*Homo sp.*,early neandertals?) together with Ceprano and Daka specimens. We employed 30 skull characters [16] under an outgroup comparison criterion by using ER3883 as outgroup. The characters are unordered and unweighted. We were not able to find any reasons to suppose that our ingroup was non-monophyletic [18, 22–24], so we assume the monophyly of outgroup plus ingroup. The character states are listed in Table 1; the character states are scored vs taxa in the matrix presented in Table 2.

The search for the most parsimonious trees was performed through tree-bisection-reconnection heuristic algorithm with random sequence addition as implemented in PAUP with ACCTRAN character-state optimisation. Node support was evaluated through a bootstrap analysis with 100 replicates. The diagnoses of the nodes were made by the DOS Equis function of the computer program Hennig86 [9, 15].

Table 1
Character states.

1	Long cranial vault: (0) yes, (1) not.
2	Low cranial vault: (0) yes, (1) not.
3	Maximum breadth across the angular torus or supramastoid crest: (0) yes, (1) not.
4	Thick vault bones (parietal): (0) not, (1) yes.
5	Pronounced postorbital constriction: (0) present, (1) absent.
6	Frontal keel or ridge: (0) present, (1) absent.
7	Straight junction of torus and frontal squama: (0) absent, (1) present.
8	Coronal ridge: (0) present, (1) absent.
9	Flattened parietal: (0) present, (1) absent.
10	Rectangular parietal: (0) absent, (1) present.
11	Low temporal squama: (0) absent, (1) present.
12	Flat superior border of the temporal squama: (0) not, (1) yes.
13	Small mastoid process: (0) yes, (1) not.
14	Opisthocranion coincident with inion: (0) yes, (1) not.
15	Sharply angulated occipital profile: (0) present, (1) absent.
16	Broad nasal bones: (0) not, (1) yes.
17	Horizontal inferior border of the supraorbital torus: (0) not, (1) yes.
18	Continuous thickness of the supraorbital torus: (0) present, (1) absent.
19	Glabellar inflexion in superior view: (0) present, (1) absent.
20	Ceprano-like “torsion” of the supraorbital torus: (0) absent, (1) present.
21	Bilateral discontinuity (ridges) of the supratoral sulcus: (0) absent, (1) present.
22	Prominent angular torus at mastoid angle: (0) absent, (1) present.
23	Marked supramastoid crests: (0) present, (1) absent.
24	Marked mastoid crests: (0) present, (1) absent.
25	Occipitomastoid ridge: (0) absent, (1) present.
26	Juxtamastoid ridge absent: (0) yes, (1) not.
27	Suprameatal tegmen: (0) present, (1) not.
28	Occipital torus with supratoral sulcus: (0) not, (1) yes.
29	Occipital torus continuous with angular torus and supramastoid crest: (0) not, (1) yes.
30	Mid-sagittal depression of the occipital torus: (0) absent, (1) present.

Table 2
Taxon × character matrix.

ER3883	000000000000000000000000000000
OH9	0000011?1000100000000111011000
Bodo	00?010110?11???11101??????????
Kabwe	00010111011101010101100110111?
Saldanha	00?0101101?1?01?010110?????010
DMN2280	000001101101101001110101??1000
DMN2282	000?00001101100?01?10101??1000
Sng2	000000101000101?10?00000101110
Sng17	000001001100101110100000111010
Zkd3	000001001000101100000100101110
Zkd10	000001001100101110100101101100
Zkd11	000001001000101110100101101100
Zkd12	000101001000101110100100101100
Ceprano	100010011011001111011100101100
Arago	00?1100110?????1000111????????
Steinheim	0011100110111110100001010110001
Petralona	00011011011100010000110???1100
At-Sh-Cr4	100010010111010100000101100111
At-Sh-Cr5	000010110011010110000101100101
Daka	100010011011001101011100101100

4.2. Results

Through the cladistic analysis, we found eight equally parsimonious trees, from which a strict-consensus tree was generated (Fig. 4). The arrangement of clades of the strict-consensus tree is as follows: a clade including OH9, DMN2280 and DMN2282; a large monophyletic group including a sub-clade of Asian *Homo erectus* from Zhou-khoudian and Sangiran, which is sister to a sub-clade including all the human forms living in Europe and Africa more recently than one million years ago. This clade, in its turn, is formed by two sister groups: one including Steinheim and the specimens from Atapuerca, and another including the following sequence of sisters: Ceprano and Daka; Arago sister to Petralona which is sister to Kabwe that, in his turn, is sister to Saldanha and Bodo.

The Ceprano skull is almost indistinguishable from Daka and both form a monophyletic group, which is characterised by one unambiguous synapomorphy (short cranial vault) and one ambiguous synapomorphy (presence of a sharply angulated occipital profile which occurs in Saldanha too). Both specimens are monophyletic with other human forms from Europe and Africa (Arago, Petralona, Kabwe, Saldanha, Bodo) based on the following synapomorphies: presence of Ceprano-like ‘torsion’ of the supraorbital torus (reverted in Arago and occurring also in the Dmanisi skulls), and presence of bilateral discontinuity of the supratoral sulcus (occurring also in Steinheim). Arago, Petralona, Kabwe, Saldanha and Bodo are monophyletic to the exclusion of Ceprano and Daka. The branching pattern shown in the strict-consensus tree suggests the Asian *Homo erectus* and the human forms living in western Europe and Africa during the Middle Pleistocene share a common ancestor, which is more recent than that shared by OH9 and the specimens from Dmanisi.

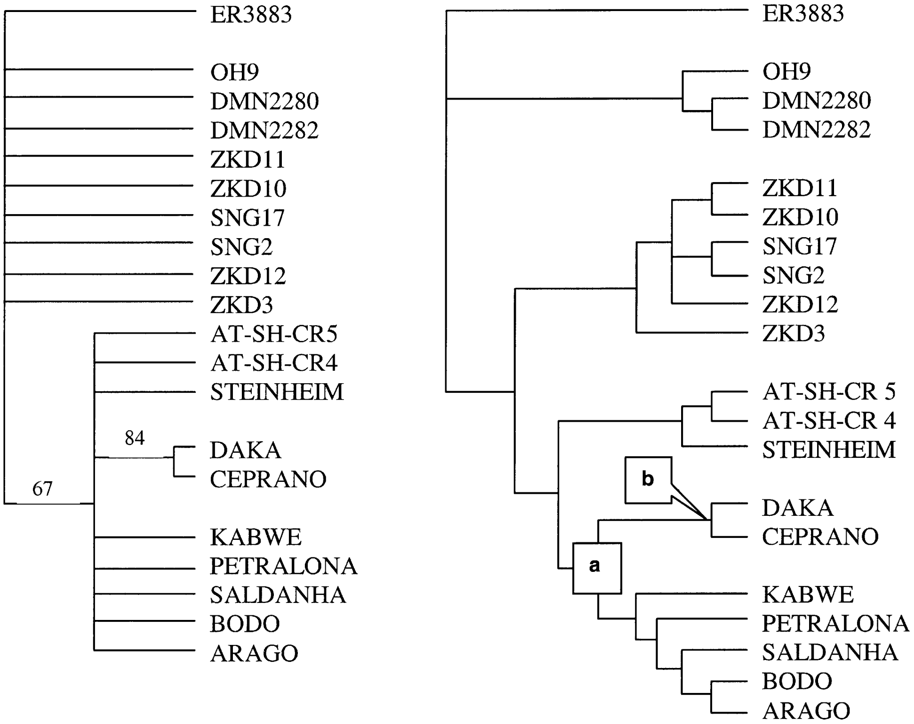

Fig. 4. Phylogenetic relationships of *Homo cepranensis*. (**a**) 50% majority rule strict consensus tree showing bootstrap values over the branches. (**b**) Strict consensus tree from eight equally parsimonious cladograms showing that Ceprano and Daka specimens form a monophyletic group (node **b**); the cladogram is 80 steps long and such as: Consistency Index = 0.3625, Homoplasy Index = 0.6375, Retention Index = 0.6434 and Rescaled Consistency Index = 0.2332; the other equally parsimonious trees differ in the resolution of Asian *Homo erectus* only. Sinapomorphies at principal nodes: (**a**) 5(1) unpronounced postorbital constriction, 20(1) 'Ceprano-like' torsion of the supraorbital torus, 21(1) presence of a bilateral discontinuity (ridges) of the supratoral sulcus; (**b**) 1(1) short cranial vault.

Fig. 4. Relations phylogénétiques d'*Homo cepranensis*. (**a**) Arbre de strict consensus qui suit une règle de majorité de 50 % et qui fait apparaître des valeurs de *bootstrap* au-dessus des branches. (**b**) Arbre de strict consensus dérivé de huit cladogrammes de même parcimonie, qui montre que les crânes de Ceprano et de Daka forment un groupe monophylétique (nœud **b**) ; le cladogramme a une longueur de 80 *steps*, avec : indice de cohérence = 0,3625, indice d'homoplasie = 0,6375, indice de rétention = 0,6434 et indice de cohérence recalibré = 0,2332 ; les autres arbres de même parcimonie sont différents seulement en ce qui concerne la résolution de l'*Homo erectus* asiatique. Sinapomorphies aux nœuds principaux : (**a**) 5(1) constriction post-orbitale non prononcée, 20(1) torsion « de type Ceprano » du torus supraorbital, 21(1) présence d'une discontinuité bilatérale (crêtes) du sulcus supratoral ; (**b**) 1(1) courte voûte crânienne.

Bootstrap values are usually low, suggesting the presence of some homoplasy in our morphological data set. Convergence is observed in some characters among which 17 (horizontal inferior border of the supraorbital torus), 18 (continuous thickness of the supraorbital torus), and 27 (suprameatal tegmen). In the 50%-majority rule strict-consensus tree, the clades described above collapse and just two of them are maintained. Here there is a large clade including Bodo, Saldanha, Kabwe, Atapuerca skulls, Steinheim, Petralona, Arago, Ceprano and Daka, within which a highly supported (87%) small clade (including Ceprano and Daka) is nested.

5. Conclusion: *Homo cepranensis* and the first peopling of Europe

The oldest evidence of human migration out of Africa is represented by the Dmanisi specimens dated to 1.7 Ma [10–12]. Ceprano and *H. antecessor* are firm evidence of a human peopling of Europe at sometime between 0.9 and 0.8 Ma.

The archaeological evidence of a continuous European settlement is under debate [21], but we can suppose at least a discontinuous presence of human populations in Europe following about 1.0 Ma, and before 0.5 Ma. Moreover, palaeontological evidence suggests that Early Pleistocene mammals migrated towards Europe from the Middle East and Gibraltar along both eastern and western migratory routes. In this scenario, since the typical characters of European *H. heidelbergensis* are absent in the frontal morphology of Ceprano, this form is a representative of an African population that migrated at about 1.0 Ma (represented by the specimen from Bouri [5] and as demonstrated by the cladistic analysis) and that did not ultimately contribute to the human population of Europe during the Middle and Late Pleistocene. On the other hand, Ceprano shares features with Middle Pleistocene *H. rhodesiensis*, and this allows us to assume that Ceprano is an early relative of this African form. The European fossils included in *Homo heidelbergensis* (Petralona, Arago etc.) retain some pleisomorphic characters (e.g., thick bony tables) that are almost completely absent in the African fossils (Kabwe, Saldanha and Bodo); in this African specimens, it is possible to observe (especially under indirect light) an evidence of a slight division between the supraciliar relief and the supraorbital trigone in the frontal torus; a hint of this character seems to appear in Ceprano too.

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