Ceprano (a "transitional" Homo calvarium)



Giorgio Manzi

Department of Environmental Biology, Sapienza Università di Roma, Rome, Italy

Ceprano is a human calvarium (calvarium, or calvaria, means a cranium without facial bones) that was occasionally found in several fragments in March 1994 near the homonymous town in southern Latium, Italy (Fig. 1). When discovered, a geo-stratigraphic approach was performed at the regional level and suggested an age of the layer of deposition close to 800-900 ka (Ascenzi et al. 1996, 2000). According to this date, in the mid-1990s, Ceprano contributed to the denial of the so-called short chronology for the earliest inhabitants of Europe (Manzi et al. 2001). In addition, the archaic features of the specimen were related to Mode 1 techno-complexes scattered in various sites across the Ceprano basin, albeit there are also Acheulean assemblages in the same area (Ascenzi et al. 1996; Biddittu et al. 2020).

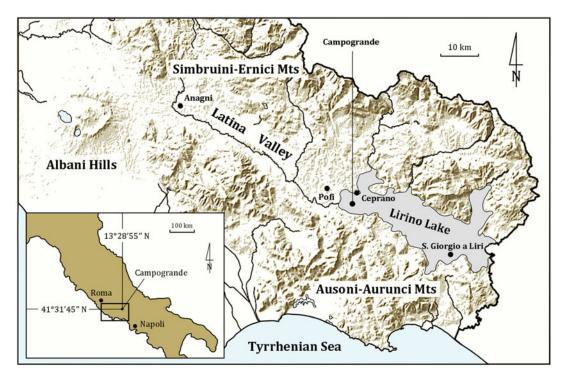
Starting from 2001, a project of field studies was developed for almost a decade, with the aim to validate the previous geo-chronological model and improve the available paleontological and archaeological records. In contrast to the expectations, the results of this multidisciplinary work consistently showed that Ceprano is more recent than previously believed, pointing to a time range

close to the beginning of MIS 11, that is, between 430 and 385 ka (Manzi et al. 2010). It was also pointed out that the Ceprano hominin died in a floodplain environment with a low topographic gradient, where a fluvial meandering channel occurred after the retreat in extension of the ancient Lirino Lake (Manzi et al. 2010; Di Vincenzo et al. 2017; Biddittu et al. 2020).

The reconstruction of the human calvarium from dozens of fragments (Fig. 2) required the combined efforts of various experts and, overall, about 5 years (Ascenzi et al. 2000). After a first attempt described in 1996, a revised one was obtained in 1999, which has been then accurately re-evaluated, documented (including a microCT-scan recording), and published in various international journals (e.g., Manzi et al. 2001).

From a taxonomic point of view, Ceprano was originally considered to be a European representative of *Homo erectus* sensu *lato* (Ascenzi et al. 1996; Clarke 2000), whereas in more recent papers its affinities were reconsidered (Ascenzi et al. 2000; Manzi et al. 2001; Mounier et al. 2011), arguing that only less than two-thirds of its character states are consistent with those that are commonly observed in *Homo erectus* and/or in *Homo ergaster* – to such an extent that the variability of these taxa considerably increases when Ceprano is added – while other traits appear more derived.

For a proper phylogenetic interpretation of Ceprano, it is necessary to take into account that different sources of data consistently point out to



Ceprano (a "transitional" Homo calvarium), Fig. 1 Location of the site where the Ceprano calvarium was discovered in 1994, along the Latina Valley near the town of Ceprano, approximately 100 km southeast of

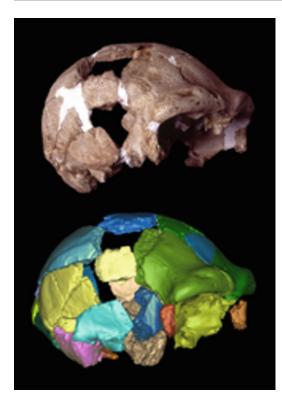
Rome; the gray area corresponds to the inferred maximum extension of the Lirino Lake during the Early/Middle Pleistocene (Biddittu et al. 2020)

the time window between 1.0 and 0.5 Ma for the emerging of a derived kind of Homo (i.e., distinct from Homo ergaster/erectus). This discontinuity most probably originated in Africa (Profico et al. 2016), from where these new humans started to spread across Eurasia, together with the Acheulean techno-complexes they made (Biddittu et al. 2020). This humanity is referred by many authors to a polymorphic and widespread single species; priority rules confer to this taxon the name of Homo heidelbergensis. In addition, in view of the occurrence of different lineages that are recognized during the Middle Pleistocene as belonging to such a putative species, it has been suggested the identification of chrono-geographic varieties or subspecies (i.e., potential incipient species) of *Homo heidelbergensis* (Manzi 2016).

Given this scenario, although the broad architecture of the Ceprano calvarium is close to the general shape that is shared by fossils referred to *Homo erectus* (sensu *lato*), a number of discrete

features may be viewed as derived, suggesting a connection with other humans of the Middle Pleistocene. Moreover, Ceprano does not display any Neanderthal trait, differently from a great part of the European samples of the Middle Pleistocene, whereas it shows affinities with penecontemporaneous African specimens (Manzi et al. 2001; Bruner and Manzi 2007; Mounier et al. 2011). Therefore, its peculiar morphology exhibits a unique combination of archaic and derived features that suggests a puzzling scenario of human evolution in Europe, which involves the occurrence of a considerable phenetic diversity beforehand the evolution of Homo neanderthalensis, but concurrently with samples clearly belonging to the Neanderthal lineage (Manzi et al. 2001; Manzi 2016).

In this light, Ceprano documents the occurrence of an archaic variety of *Homo heidelbergensis*, whose cranial morphology was partially lost along the subsequent trajectory of human evolution in Europe. By contrast, this morphology was



Ceprano (a "transitional" Homo calvarium), Fig. 2 The Ceprano calvarium (above) and its digital reconstruction (Di Vincenzo et al. 2017)

preserved elsewhere: namely, in Africa and in mainland Asia. Given this scenario, the hypothesis is that the Italian specimen was confined in an eco-geographical *refugium* and retained features of the ancestral stock of *Homo heidelbergensis*. This original morph, in turn, gave rise to the hominin variability observed during the Middle Pleistocene and was ancestral to modern humans (*Homo sapiens*), in Africa, as well as to the Neanderthals (*Homo neanderthalensis*), in Europe, and the so-called Denisovans, in Northeastern Asia.

In conclusion, in view of the shape and morphological features displayed by Ceprano, it may be assumed that this specimen represents the best candidate available at present to describe the ancestral cranial morphology of the still largely unknown original variety of *Homo heidelbergensis* (Bruner and Manzi 2007; Mounier et al. 2011), which may be referred to as the stem chrono-subspecies of this taxon to be

named *Homo heidelbergensis heidelbergensis* (Manzi 2016).

Cross-References

- **▶** Evolution
- ► Fossil Record
- ▶ Homo erectus
- ► Homo ergaster
- ► Homo heidelbergensis
- ► Homo neanderthalensis
- ► Homo sapiens
- ► Paleontology
- ► Refuge

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