

## Review Article

# Before the Emergence of *Homo sapiens*: Overview on the Early-to-Middle Pleistocene Fossil Record (with a Proposal about *Homo heidelbergensis* at the subspecific level)

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The origin of *H. sapiens* has deep roots, which include two crucial nodes: (1) the emergence and diffusion of the last common ancestor of later *Homo* (in the Early Pleistocene) and (2) the tempo and mode of the appearance of distinct evolutionary lineages (in the Middle Pleistocene). The window between 1,000 and 500 thousand years before present appears of crucial importance, including the generation of a new and more encephalised kind of humanity, referred to by many authors as *H. heidelbergensis*. This species greatly diversified during the Middle Pleistocene up to the formation of new variants (i.e., incipient species) that, eventually, led to the allopatric speciation of *H. neanderthalensis* and *H. sapiens*. The special case furnished by the calvarium found near Ceprano (Italy), dated to 430–385 ka, offers the opportunity to investigate this matter from an original perspective. It is proposed to separate the hypodigm of a single, widespread, and polymorphic human taxon of the Middle Pleistocene into distinct subspecies (i.e., incipient species). The ancestral one should be *H. heidelbergensis*, including specimens such as Ceprano and the mandible from Mauer.

## 1. Introduction

The origin of anatomically and genetically modern humans (*H. sapiens*) from a small population of “archaic” *Homo* is an event reasonably well set in sub-Saharan Africa around 200 thousand years before present (or ka) [1–3]. Nevertheless, this event has deep roots in the Middle Pleistocene, primarily at the time of the divergence between the evolutionary lineage of our own species and that of the Neanderthals—between approximately 800 and or 520 ka, according to Briggs and coworkers [4] (compare [5]), or between 538 and 315 ka, according to Endicott and colleagues [6]—and even earlier, in the late Early Pleistocene, when the common ancestor of both *H. sapiens* and *H. neanderthalensis* emerged and began to spread geographically.

This paper aims at investigating such a new frontier for paleoanthropology. It will focus on topology, chronology, tempo, and mode of the main evolutionary nodes before the appearance of *H. sapiens*.

When considering all the available data, we are confronted with a comprehensive scenario about the deep roots of our species. At the same time, it becomes possible to approach the issue from regional and/or local perspectives [7]. The special case study provided by a well-known fossil specimen from Italy—that is, the calvarium from Ceprano (for a review, see [8])—may help to see the remote origins of *H. sapiens* from an interesting and helpful perspective.

## 2. Old and New Paradigms

*2.1. The Midcentury View.* Views about the origin of our own species greatly changed during the last couple of decades, involving our interpretation of the evolution of the genus *Homo* as a whole. The paradigm of mid-20th century, shared among many scholars until recently, was based on the existence of a single human species that evolved gradually and sequentially during the entire Pleistocene: it is the so-called “single-species hypothesis,” influenced by

the gradualist perspective of the “modern synthesis” [9, 10]. Consistently with this perspective, the current human diversity would have been the result of small and constant changes among populations and within the species as a whole (viewed as a single, extremely large population) taking place from the original geographical diffusion of the genus *Homo*, where the roots of the present human diversity would be found.

According to this view, successive stages and/or regional variants were implied within a widespread archaic species—*H. erectus*—and subsequently among *H. sapiens*. The result was a model of either progressive or regional changes that, with the persistence of a single polymorphic humanity in each span of geological time, was evolving towards variants of the modern species and, ultimately, to the present human “races” [11]. As a consequence, the taxon *H. sapiens* included the extant humankind, but also extinct morphotypes like the Neanderthals in Europe and the Near East as well as, more in the depth of the Middle Pleistocene, diverse archaic humans in Africa, and in eastern Asia, collectively referred to as “archaic *H. sapiens*.” Thus, under the same specific name, *H. sapiens*, each of these morphs was ascribed to a different subspecies, with the adoption of a trinomial nomenclature that gave rise to nomina such as *H. sapiens neanderthalensis* and *H. sapiens sapiens*.

The theory called “multiregional evolution” is a good example of this view. It is well known that according to the model introduced by Wolpoff and colleagues [12] the anatomically modern populations of Africa, Asia, and Europe have been viewed as emerging in continuity with the preceding archaic humans of the same geographical area. This hypothesis was based on the observation that a certain degree of “regional continuity” characterizes the morphologies of archaic and modern populations within each geographical area. This observation, however, has been contradicted by a number of works [13, 14] and, more in general, the model is regarded as not in agreement with most of the paleogenetic data (since the seminal work by Cann et al. [15]).

To a large extent, this view has now been abandoned, after a debate that lasted for more than two decades [16]. Some of the issues of this scientific revolution (*sensu* Kuhn [17]) may be summarised with reference to Figure 1 and are briefly discussed below.

**2.2. A New Scenario.** One of the consequences of the middle-century paradigm on the interpretation of the fossil record was that a single species, *H. erectus*, included a largely distributed, archaic-looking, and polymorphic humankind that was ancestral to modern humans. It was considered to be the first hominid species that left Africa, equipped with a brain of about 1,000 ml and skilled enough to produce the elaborated stone tools of the Acheulean, and able to face different climatic and environmental conditions because of its behavioural and technological—someone says “cultural”—aptitudes. In brief, *H. erectus* was viewed as the quasimodern “hero” who “conquered” the Old World: an authentic “dawn of humanity.”

However, an increasing number of data—including the evidence coming from the Georgian site of Dmanisi [18, 19]—suggests a different scenario. Those that were responsible for the first out-of-Africa diffusion were not derived, encephalised, and technologically advanced humans, but more archaic hominins, with a brain just above the threshold of 500–600 ml (maximum encephalic volume of the australopithecines) and morphologically close to the changing definition and hypodigm of *H. habilis* (after Leakey et al. [20]). Driven by ecological rather than behavioural or “cultural” motives, these hominins had a tendency—which was new with respect to *Australopithecus*, *Paranthropus*, and the Primates in general—to diffuse and adapt to variable, nontropical environments. The same corpus of data suggests that this process should have started well before the appearance of either *H. erectus* or the Acheulean (which are now viewed as separated and independent phenomena), that is roughly between 2,000 and 1,500 ka.

Within this new approach, *H. erectus* may be viewed as a Far Eastern (Java and China) species only (*contra* Asfaw and colleagues [21]) whereas their African counterparts are considered as a distinct species, *H. ergaster* [22, 23]. Alternatively, these two geographical variants are grouped under the definition *H. erectus sensu lato*, while *H. erectus sensu stricto* would be the Asian deme of such a multiregional taxon. At the same time, other species have been named or old nomina have been reconsidered, and they include (according to the chronological order of references that are pivotal for the present debate): *H. rudolfensis* [22], *H. heidelbergensis* [24], *H. antecessor* [25], *H. helmei* [26], *H. mauritanicus* [27], *H. rhodesiensis* [28], *H. georgicus* [29], *H. cepranensis* [30], and *H. floresiensis* [31]. However, many of these taxa are debated and/or not widely acknowledged; thus, the generally accepted scenario is far less “speciose” than it might appear from such a tentative list.

Although the identification of all these different species clearly implies an overestimation of interspecific diversity—that in many cases was more probably intraspecific (see below)—this plethora of nomina is in accordance with a scenario that foresees the geometry of an “adaptive radiation,” describing the generation from a common stem of a great variability, in space as well as in time. Moreover, this confers a clearer, more intelligible significance to human varieties that were formerly hidden, being referred either to *H. erectus* (*sensu lato*) or to the informal and confusing entity called until recently “archaic *H. sapiens*” (which has been abandoned and has almost disappeared from the literature).

Looking at Europe, the relatively best known regional example, at least two distinct waves of immigrants seem to be recognizable between the late Early and the early Middle Pleistocene. In terms of fossil record, the former wave is documented at present only in Spain and is referred to *H. antecessor*. As a matter of fact, this species occurs in two sites of the Sierra de Atapuerca, near Burgos: in the layer TE9 of the Sima del Elefante, dated to about 1,200 ka [32], and in the layer TD6 of the Gran Dolina, dated to more than 780 ka [25]. These humans are in association with the so-called “Oldowan” (or Mode 1 of the Lower Paleolithic [33]), largely diffused in a number of sites of Mediterranean and

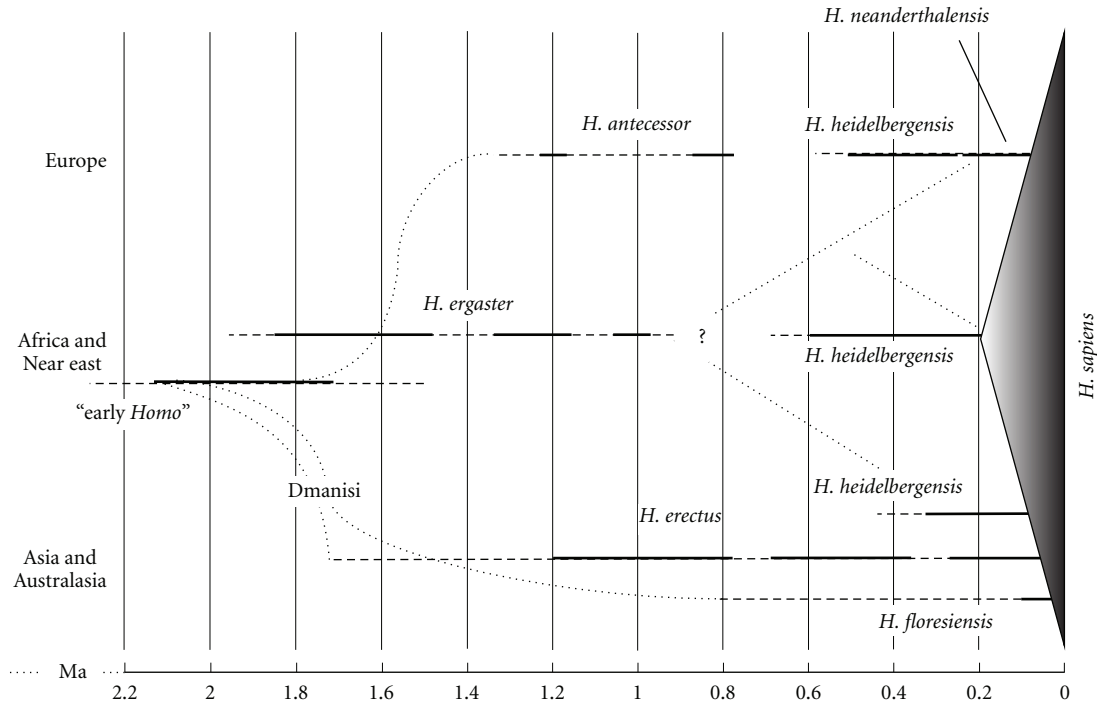


FIGURE 1: Evolutionary tree of the genus *Homo* illustrating trajectories of the diffusion and/or tentative phylogenetic relationships between a limited number of species. Note that, according to this scenario, only *H. sapiens* and *H. heidelbergensis* (not *H. erectus*) have a widespread distribution in Africa and Eurasia. Also what is called here “early *Homo*” (*H. habilis*? Primitive *H. ergaster*?) might have been largely distributed at the beginning of its dispersal (i.e., well before 1 Ma). Legend. Continuous bold lines: time-span covered by species in different regions; dashed lines: inferred extension of specific time limits, although the evidence may be missing, dubious, or controversial; dotted lines: phylogenetic links and/or trajectories of diffusion.

continental regions [34]. In addition, their settlements could have been discontinuous until about 600 ka, being strongly influenced by ecological conditions [35].

Seemingly, the latter possible dispersal into Europe was more recent than 700–600 ka and related to morphologically derived hominids, with clear signs of further encephalization, which are well known from a number of sites. The most notable assemblage of fossil material is again in the Sierra de Atapuerca [36], namely, at the site with the evocative name of Sima de los Huesos, or SH, whose extraordinarily rich and well-preserved human sample has been pushed back to about 600 ka [37]. These fossils are generally included within the species *H. heidelbergensis*, which is usually, but not always, associated with Mode 2 (or “Acheulean”) Paleolithic assemblages.

*H. antecessor* and *H. heidelbergensis* compete, one against the other, for the same phylogenetic position in current evolutionary trees of the genus *Homo*, viewed as provisional, alternative models of human evolution. *H. antecessor* is regarded by the Spanish workers (after [25]) as the stem species that was ancestral to the evolutionary divergence within the late natural history of the genus *Homo*, leading to the evolution of the Neanderthals in Europe and to the emergence of our species in sub-Saharan Africa. Alternatively, it is *H. heidelbergensis* to be claimed for the same crucial role [24]. In a sense, the Sierra de Atapuerca provides the evidence that could explain this ambivalence, either in the former or

in the latter direction. At the same time, however, it should be remarked that the material from Sima de los Huesos is clearly Neanderthal oriented, being characterized by a number of features that, later in the Pleistocene, will become typical of the Neanderthals [38, 39]. Looking at the material from Atapuerca SH, therefore, *H. heidelbergensis* acquires the identity of a European regional chronospecies in continuity with *H. neanderthalensis*, which appears inappropriate as also ancestral to the African lineage leading to *H. sapiens*. There are, anyway, in Europe other fossil specimens—such as the calvarium from Ceprano, Italy (see discussion below)—that are penecontemporaneous with the material from Atapuerca SH and might represent (far better than the Spanish sample) a possible ancestral morphotype for *H. heidelbergensis*, if we look at this species as the evolutionary stem before the divergence between Neanderthals and modern humans (compare [6]).

Moving to Africa, it has been shown [8, 23] that specimens dated to about 1,000 ka or slightly less—such as Daka, Buia, and Olorgesaille—share phenetic affinities closer to *H. ergaster* than to Middle Pleistocene African hominins—like Bodo and Kabwe—which are referred to *H. heidelbergensis* or, alternatively, to *H. rhodesiensis*. Hence, these sub-Saharan specimens of the late Early Pleistocene signal a morphological discontinuity with the subsequent fossil record and should be considered as late representatives of *H. ergaster*. In addition, as emphasized in Figure 1, the

period between 900 and 600 ka is unfortunately very poor of fossil evidence in sub-Saharan Africa, and not only there. Thus, the differences occurring between *H. ergaster* (until 900 ka) and *H. heidelbergensis* (after 600 ka) might also suggest an allochthonous origin of the latter species.

More in general, late *H. ergaster* representatives are also distinct from the Middle Pleistocene fossil record from either Europe—including the Italian calvarium from Ceprano (contra Mallegni and coworkers [30]) as well as the assemblage from Atapuerca SH—or mainland Asia, looking at specimens like Narmada, Dali, and Jinniushan. These, in turn, are also respectively distinguishable from *H. antecessor*, in Europe, and from *H. erectus* sensu stricto in China (e.g., the fossil sample from Zhoukoudian near Beijing) and Java. We still do not know where, but it seems that something happened between about 1,000 ka and 500 ka that was capable to generate—in sub-Saharan Africa, Europe, and mainland Asia—a new and more encephalised kind of humanity, which was different from the variability coming from the earliest human dispersal out of Africa: that is, *H. ergaster*, *H. antecessor* and *H. erectus* (leaving aside the singular, intriguing case of *H. floresiensis* [31]).

To sum up, at present, the chronology, topology, and phylogenetic dynamics related to the geographically dispersed and rather synchronous appearance of Middle Pleistocene humans—or *H. heidelbergensis*, viewed as a single widespread species—are still unclear. Ultimately, the provenience of those archaic humans (see question mark in Figure 1) that, in turn, were ancestral to the origin of both Neanderthals and modern humans is not evident [1, 40, 41].

A possible answer comes from the results recently obtained with the analysis of the complete mitochondrial DNA (mtDNA) sequence retrieved from the isolated human phalanx of the Denisova cave in the Altai mountains, southern Siberia. In the context of episodic occupations of this site in the Late Pleistocene, the layer where the phalanx was found has been dated to 48–30 ka, in association with an archaeological assemblage including both Middle and Upper Palaeolithic elements. The mtDNA evidence surprisingly points to humans that were different from both *H. neanderthalensis* and *H. sapiens*, but share with them a common ancestor around 1,000 ka [42]. As a working hypothesis, this suggests that the Denisova phalanx may represent an unknown type of hominin that reached mainland Asia during a diffusion that begun (where, we do not know) about 1 million years ago; this humankind was in close phylogenetic relationship with the last common ancestor of Neanderthals and modern humans and survived in north-eastern Eurasia at least until about 40 ka. As visible in Figure 1, the origin of these three clades corresponds well to the morphological discontinuity occurring in the fossil record before the appearance of *H. heidelbergensis*.

Researchers opted to wait for their data to provide a clearer picture of the relationship with Neanderthals and modern humans before giving the hypothetical unknown species a formal name. Nevertheless, it is already possible to speculate that the Denisova hominins were in relation with the “non-*erectus*” occupation of mainland Asia during the Middle Pleistocene. Assuming in fact that *H. erectus* was

one of the evolutionary outcomes of the earliest diffusion in Eurasia, prior to 1,500 ka (see Figure 1)—and excluding, therefore, this taxon from the scope of possibilities—we have to look elsewhere and focus on Asian Mid-Pleistocene specimens such as Dali and Jinniushan, in the past ascribed to *H. sapiens daliensis* [43] and currently considered by some authors as the easternmost variant of *H. heidelbergensis* (after Rightmire [24, 40]). Now, should it be appropriate to ascribe the phalanx from Denisova and its precious molecular content to a late variant of the same taxon as Dali Jinniushan and other “non-*erectus*” specimens from the late Middle Pleistocene of Mainland Asia?

Further analyses on the Denisova material—including exceptionally preserved nuclear DNA from the phalanx and the discovery of an upper molar—drove the same group of researchers to publish additional data [44], which appeared when the present paper was under revision. They confirmed that the Denisova individuals, and the population they belonged to, exhibit molecular (mtDNA) as well as morphological (dental) features that appear extremely archaic. By contrast, the picture that emerges from the analysis of the nuclear genome suggests that this human group has close affinities with the Neanderthals, larger than expected from the mtDNA. Eventually, the model they suggest is that the Denisova hominins are a sister group to Neanderthals, “with a population divergence time of one-half to two-thirds of the time to the common ancestor of Neanderthals and modern humans” (Reich et al. [44, page 1057]). At the same time, Reich and colleagues [44, page 1057] admit that “other, more complex models could also explain the data.” Actually, in my view (as it will be reported in Figure 2), the same corpus of data may be explained with the occurrence of gene flow across Eurasia between the ancestors of both the Neanderthals and the Denisova hominins along the mid part of the Middle Pleistocene.

Paleogenetic data also indicate that trajectories of human evolution leading in Europe to the Neanderthals and in Africa to modern humans coalesced around 500 ka [4–6]. This substantiates previous conclusions based on morphology and palaeogeography, which suggested isolation and divergence between the European and African lineages during the Middle and the early Late Pleistocene (after Santa Luca [38]). As a matter of fact, looking at the hypodigm of *H. heidelbergensis* as a whole, it is clear that a considerable amount of variability characterises this putative species—bearing regional features in Africa, Asia, and Europe, respectively, [47]—referable to a phenomenon known as “isolation by distance” [48]. At the same time, phenotypic variation has to be noted also at the regional level, such as within the European fossil record of the Middle Pleistocene, now greatly expanded by the recently revised chronology of the calvarium from Ceprano [49].

### 3. The Case Study of Ceprano

**3.1. A Cranium for the Earliest Europeans?** At present, there is a general consensus in assuming that humans spread towards western Europe during the late Early Pleistocene,



probably earlier than 1,200 ka. This is demonstrated by recent findings in Spain [32, 50], and possibly in southern France [51] and Italy, where the earliest settlements are suggested by the stone tools found at Pirro Nord, near Apricena in Puglia (southern Italy) [52, 53], in association with a rich paleontological assemblage biostratigraphically referred to a Faunal Unit of the Early Pleistocene (about 1,400 ka; [54, 55]). Of interest are also sites dated at around 1,000 ka such as Monte Poggiolo [56] or a number of localities in the Ceprano basin and surroundings that have been recently object of a new season of excavations and analyses [57]. Between 950 and 700 ka, these humans proved to be capable to reach and adapt to higher latitudes, as demonstrated by sites in southern England [58].

Less than 20 years ago, at the beginning of the 1990s, the available data were not so clear, and a model of “short chronology” for the earliest inhabitants of Europe was put forward [59], indirectly supported by the finding of the human tibia from the Acheulean site of Boxgrove [60]. In brief, the “short chronology” hypothesis postulated that no humans were present in Europe before the time limit of approximately 500 ka, a date that is close to the putative chronology of the mandible from Mauer (holotype of *H. heidelbergensis*), which remained for about one century the most ancient fossil hominin north of the Mediterranean Sea. This date is also consistent with the earliest clear documentation of Acheulean assemblages spread in various part of the continent from at least 600 ka [61].

One year after the discovery at Boxgrove, hard evidence from Italy (Ceprano, March 1994) and Spain (Atapuerca TD6, July 1994) chronologically referred to more than 700–800 ka [62, 63], suddenly falsified the hypothesis of a “short chronology.” Thus, together with the Gran Dolina material, the calvarium found near Ceprano was considered for more than a decade part of the most ancient fossil evidence of the human presence in Mediterranean Europe, suggesting the tentative attribution of Ceprano to *H. antecessor* [27] or, alternatively, the occurrence of two different human species in Europe during the late Early Pleistocene [30, 62, 64–66].

The Italian specimen was discovered in several fragments in a field known as Campogrande, near the town of Ceprano, in southern Lazio, less than 100 km south-east of Rome. Its discovery represents the result of systematic field activities conducted for decades in southern Lazio by the Italian Institute of Human Palaeontology (under the supervision of the Soprintendenza Archeologica del Lazio), and particularly by I. Biddittu. On March 13th 1994, Biddittu found a first cranial fragment during a survey along the trench excavated for a new road while other portions of the same cranium were still included in the nearby section created by the excavators. Subsequently, all the fragments (about fifty) were carefully extracted and sieved from the clayey sediments. The reconstruction of the cranium required more than one attempt, the intervention of a composite team, and, overall, about five years [62, 64, 67].

For the purpose of a chronological reference, the geologist A. G. Segre [62, 67] suggested a compilation stratigraphic column at a microregional scale, mainly based on previous geopalaeontological knowledge. This describes two main

complexes; the layer where the human calvarium was found belongs to the lower portion of the upper stratigraphic complex, pointing at a tentative age of about 800–900 ka. Consistently, the archaic features of the calvarium were considered in association with Mode 1 technocomplexes coming from sites scattered in the Ceprano basin [57], although a number of Acheulean assemblages are also well known at Campogrande and surroundings and are now submitted to an accurate reappraisal [49].

*3.2. A Tantalizing Specimen of the Middle Pleistocene.* With these premises, a project of surveys and excavations started in 2001 under the direction of I. Biddittu and G. Manzi, with a threefold aim: (1) a better comprehension of the Pleistocene stratigraphy of the Ceprano basin; (2) validation of the geochronological model set by A.G. Segre; (3) improvement of the palaeontological and archaeological records. After ten years, the results obtained through a multidisciplinary approach—including stratigraphic and palynological data, combined with sedimentology, geochemistry, soil-micromorphology, taphonomy, and the archaeological evidence—showed that the Ceprano calvarium is more recent than previously believed, pointing at a time range close to about 400 ka and, more precisely, to the interval at the beginning of marine isotopic stage (MIS) 11 bracketed between 430 and 385 ka [49]. This result is also consistent with the normal geomagnetic polarity recorded in the area of discovery down to a depth of about 50 metres [68].

These unexpected results and the consequent new chronology of the fossil specimen in the mid of the Middle Pleistocene led Manzi and colleagues [49, page 584] to guess that “the morphology of the human calvarium from Ceprano—which lacks Neanderthal traits and does not have a real counterpart among the continental penecontemporaneous fossil record—now appears tantalizing. It adds an amount of unexpected diversity into the range of variation known for the European populations of the Middle Pleistocene,” and to suggest the evaluation of “more complex scenarios of human evolution in Europe than previously believed, involving either the occurrence of a considerable intraspecific diversity (with archaeologically distinct settlements) or, alternatively, the coexistence of different lineages (with their own respective archaeological traditions) during part of the Middle Pleistocene.”

This also calls for a taxonomic re-evaluation of the Italian specimen. Originally, Ceprano was attributed to “late *H. erectus*” [62, 64]. Five years later, two papers criticized the *H. erectus* affinities that were originally claimed [27, 67], reaching the conclusion that less than two-thirds of the character states in this calvarium are in accordance (and not always unequivocally) with those commonly encountered in *H. erectus sensu stricto* while others appear peculiar and/or progressive. Further studies included a cladistic approach, with the questionable proposal of a new species name [30]. Moreover, the CT scanning of the specimen [65] and other phenetic data [8, 23, 66] produced additional elements that were useful to better understand the specimen in a comparative framework.

On the whole, these researches largely support conclusions preliminarily reached by Manzi and colleagues [27], which may be summarised as follows. First of all, though some metric and architectural features of Ceprano approach those shared by fossils referred to *H. erectus*, the variability of this taxon appears greatly enlarged when Ceprano is added. Second, there are discrete features that detach Ceprano from its general “*erectus*-like” appearance and may be viewed as derived, suggesting a connection with the Middle Pleistocene fossil record from Africa and Europe. Third, Ceprano does not display any Neanderthal trait, while it shows affinities with the African pencontemporaneous fossil record, closer than the affinities it has with its European counterparts. A possible conclusion is that Ceprano may be regarded as a mosaic morphological link between the clade composed by the group of species referred to as *H. erectus* sensu lato, on the one hand, and samples commonly referred to as *H. heidelbergensis*, on the other. This in turn suggests that Ceprano might document “the occurrence of an ancestral stock of *H. heidelbergensis/rhodesiensis*” [66, page 365], whose cranial morphology was lost in part along the subsequent trajectory of human evolution in Europe, but preserved elsewhere (including Africa and, possibly, mainland Asia). In addition, it has to be remarked that Mounier and colleagues [47, 69], in the wide framework of a recent reappraisal of the fossil record pertaining to *H. heidelbergensis* and related species, provide robust and independent support to these conclusions.

#### 4. Mediterranean Perspectives

Viewed in a wide paleoecological scenario, the earliest dispersal of human groups towards the western Mediterranean regions was likely part of the progressive faunal renewal that involved the diffusion of some large mammals of African and Asian origin during the Early Pleistocene [7, 35, 70]. This diffusion was also favoured by the opportunistic nature of hominins that were *archaic* both in their morphology—highlighted by the affinities observed between the *H. antecessor* specimen from Atapuerca TE9, and the fossil sample from Dmanisi [32]—and for their inferred behaviour, as documented by Mode 1 assemblages [34]. An even more favourable window for human presence in Europe likely opened around 1,000 ka and later, when more consistent settlements were probably related to the major faunal renewal that characterised the Early to Middle Pleistocene transition. This transition—the so-called “Mid-Pleistocene Revolution” (approximately from 1,200 to 600 ka [71])—marks a dramatic change in the Earth’s climate system and represents a major episode in mammal fauna reorganization in the course of the Cenozoic, not only in Europe [72–74]. Thus, since at least 1,300 ka, dispersals of taxa and turnover phases led to a progressive reconstruction of mammalian faunal complexes in Europe that was complete after the beginning of the Middle Pleistocene [75].

The unique hominin hard evidence in Europe for this time period is represented so far at Atapuerca TE9 and TD6,

but the presence of human populations is documented by a number of Mode 1 archaeological sites. It is possible that diffusion waves, presumably scattered in time and space, led to the arrival of archaic humans in western Eurasia until MIS 16, one of the worst glaciations of the last million years, with an ice sheet extension below 50° latitude in Eastern Europe [76]. This climatic collapse probably constituted a strong environmental barrier and might not be by chance that it preceded the appearance of the Acheulean tool technology (Mode 2) in the continent. In other words, it is in the framework of the changed environmental scenario implied by the Mid-Pleistocene Revolution, but only after MIS 16, that we have clear evidence in Europe of a second main dispersal of hominins: those bearing the Mode 2 technocomplexes (for a recent review, see [1]).

The exact origin of these humans is still not clear, though it may be assumed that they ultimately emerged from Africa [42, 77]. As already stressed in the first part of this paper, these Acheulean-bearing humans exhibit a clear discontinuity in morphology with the hominins previously diffused into Europe, that is, with *H. antecessor* and/or related species. As a result of this second main diffusion towards western Eurasia, in the middle part of the Middle Pleistocene, we find in the continent a variety of human fossil samples, which are dispersed from northern (e.g., Swanscombe in England, Mauer, and Bilzingsleben in Germany, etc.) to southern latitudes (e.g., Atapuerca SH in Spain, Arago in southern France, Petralona in Greece, etc.), Italy included (e.g., Ceprano, Venosa, and Visogliano). On the whole, this fossil record is considered by many authors as part of the hypodigm of the species *H. heidelbergensis* created on one of these specimens, that is the Mauer mandible [40, 47, 78].

Subsequently, the observed pattern of evolution in Europe during the Middle Pleistocene is consistent with a long period of isolation for humans north of the Mediterranean Sea, which seems to be supported on both morphological and genetic grounds [3, 5, 38, 45, 79]. These populations are characterised by an apparent increase of Neanderthal features; an increase that, in turn, was probably related to the dramatic glacial periods of MIS 12–6, that might have produced demographic crashes among human populations, which resulted in population bottlenecks, likely favouring either genetic drift or adaptations to cold climatic conditions. Consequently, according to the so-called “accretion model” [1, 39, 80], as suggested also by studies on the Saccopastore Neanderthals and other Mid-to-Late Pleistocene fossil specimen [81–83], the European evolutionary lineage eventually led to the origin of *H. neanderthalensis* throughout successive genetic bottlenecks.

On the other hand, however, more recent evidence on the European fossil record of the Middle Pleistocene hardly supports the hypothesis of a linear and gradual process of change [84–86]. Just to give an example, endocranial metric variations fail to demonstrate the occurrence of sequential discrete steps along this hypothetical anagenetic process [87]. Moreover, the Neanderthals—even in their earliest representatives, such as those from Saccopastore—seem to be

characterized by a well-defined brain morphology, emphasizing the phylogenetic independence of *H. neanderthalensis* from *H. heidelbergensis* [83]. This suggests a distinction between two different chronospecies as well as an event of speciation that occurred in Europe towards the end of the Middle Pleistocene, which appear consistent with the paleogenetic data [4, 6].

It is reasonable that something similar—although not identical—happened with the locally evolving populations of late *H. heidelbergensis* in Africa and in Asia. An example might be the emergence in Africa of *H. sapiens*. However, the pattern in this case was peculiar in terms of both evolutionary modalities and changes in morphology. Various scholars have argued, and partly proved, that the allopatric speciations involved in the phenotypic and genetic distinction between Neanderthals and modern humans would reflect crucial differences in the respective ontogenetic processes [88–90]. Although similar trends of encephalization characterize (quantitatively) the two derived species, they diverge in many respects, particularly when we look at the shape more than at the dimensions. As a matter of fact, while Neanderthal morphology combines a fundamental archaic shape of the cranial vault with enlarged brain dimensions, the modern architecture appears completely redesigned in terms of “globularity” [91]. It has been observed, for instance, that the Neanderthals share with more archaic humans the same endocranial model, based on a single allometric trend whereas the modern range of variability implies a peculiar morphological pattern, with a larger amount of parietal development [92]. In this light, we may argue that a certain level of “allometric stasis” has occurred during the evolution of the genus *Homo* and that the exception is represented by the transition to the new phenotypic and ontogenetic equilibrium associated with the emergence of *H. sapiens*, which appears as a sharp disruption within the pattern of evolution of the genus *Homo* taken as a whole.

## 5. Summary and Conclusions

In this paper, we dealt with arguments concerning the evolution of the genus *Homo* and attempted to put recent and less recent studies in such a broader context.

As stated in the introduction, the aim was to investigate a new frontier for paleoanthropology. This is represented in my view by the discovery of the deep roots for the origin of modern humans in the Early and Middle Pleistocene, respectively, when the common ancestor of both *H. sapiens* and *H. neanderthalensis* began to spread geographically, and when the divergence between the evolutionary lineage of our own species and that of the Neanderthals occurred. In this framework, I speculated that any scenario dealing with the evolution of the genus *Homo* between the Early and Middle Pleistocene must envisage that the fossil specimen from Ceprano, Italy, does not appropriately fit into the known ranges of variability of recognized hominin species, particularly (but not exclusively) in the light of its dating to less than 430 ka. By contrast, it represents a puzzling

mosaic of plesiomorphic and apomorphic features, which might be explained according to the following “keywords”: (a) Europe; (b) Middle Pleistocene; (c) morphology “intermediate” between *H. erectus* sensu lato and *H. heidelbergensis*; (d) affinities with penecontemporaneous samples from both sub-Saharan Africa and mainland Asia.

I also observed that something that was crucial for the evolution of the genus *Homo* happened around the beginning of the Middle Pleistocene, between about 1,000 ka and 500 ka. Looking at the fossil record in Africa and Eurasia, in fact, there are differences that occur between the late representatives of the earliest spread of the genus *Homo* (e.g., *H. ergaster*, *H. erectus*, and *H. antecessor*), on one hand, and *H. heidelbergensis* viewed as a largely diffused species of more derived humans, on the other.

Thus, when connecting all the elements described in this brief overview on the Early-to-Middle Pleistocene fossil evidence preceding the emergence of *H. sapiens*, I point out that there is a single cranial specimen among the potential hypodigm of *H. heidelbergensis* [69]—that is, the calvarium from Ceprano—that is sufficiently archaic and peculiar with respect to the penecontemporaneous fossil record to represent the ancestral morphotype of this species. Moreover, it should be added that the hypodigm of *H. heidelbergensis* shows a considerable amount of variability, in which regional features may be recognised [47, 69] while phenotypic variations are observed also locally such as within the European fossil record [49]. This supports the conclusion that Ceprano would document at present, better than other specimens, a possible ancestral stock of *H. heidelbergensis*, close in time [6] to the evolutionary divergence between Neanderthals and modern humans.

These and other arguments (compare Section 2.2 for discussion and references) greatly expand, at least tentatively, the phylogenetic significance, the geographic distribution, and the time span covered by *H. heidelbergensis* viewed as a taxon that was both geographically widespread and morphologically diversified (Figure 2). Actually, it was so widespread and so diverse that inappropriately it would be referred to a single taxon, without further internal distinctions. At the same time, however, there are several signs that inbreeding among different demes of such a large biological entity were possible.

In conclusion, it seems to me that the time is ripe to introduce a trinomial nomenclature for this species. Furthermore, as stated for instance by Mayr [93, page 155]: “every species that developed through geographic speciation had to pass through the subspecies stage.” *H. heidelbergensis* includes in fact the clear occurrence of regional incipient species, which prelude to allopatric speciations such as those of *H. neanderthalensis* (in Europe) and *H. sapiens* (in Africa). Also, from this perspective, the use of subspecific ranks within *H. heidelbergensis* appears more than appropriate, as well as practical in distinguishing between demes.

My proposal is to consider the single widespread species that was ancestral to both Neanderthals and modern humans (and the “Denisovans” [44]) as fractioned in chronological subsequent and/or geographically distinguished subspecies. With reference to Figure 2 and using already available

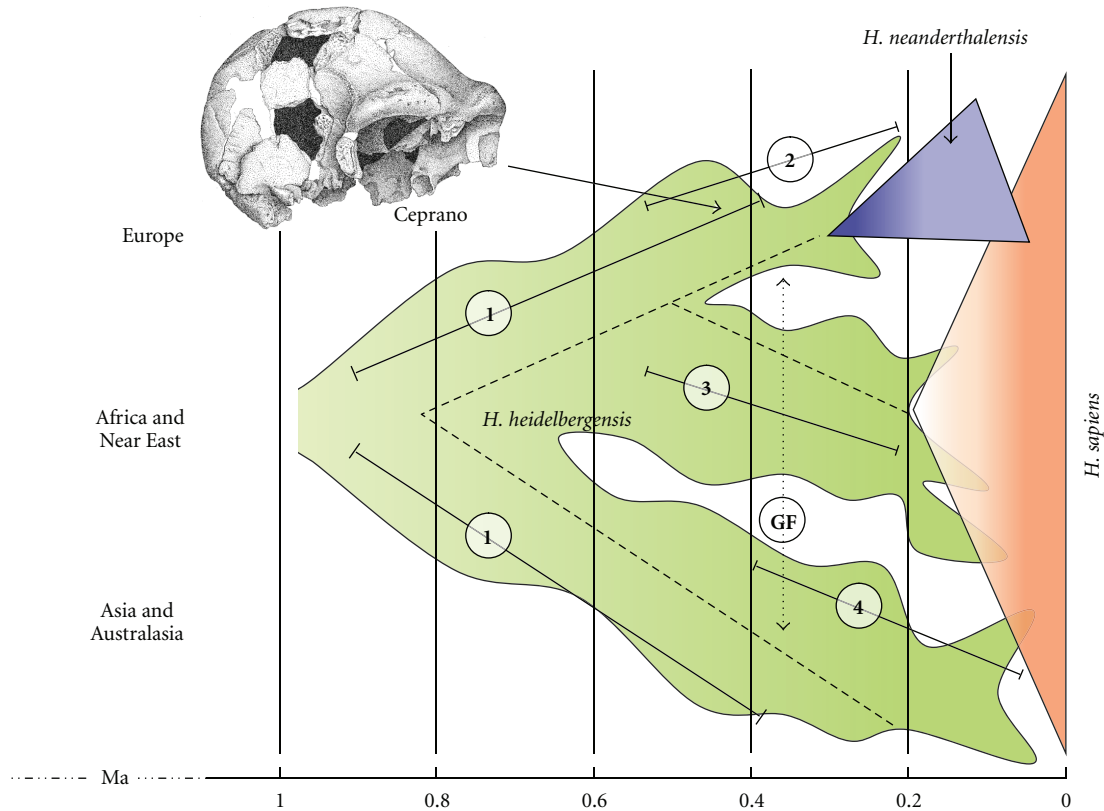


FIGURE 2: Evolutionary tree of *H. heidelbergensis* distinguished in subspecies, as suggested in this paper: (1) *H. h. heidelbergensis*; (2) *H. h. steinheimensis*; (3) *H. h. rhodesiensis*; (4) *H. h. daliensis*. The main evolutionary trajectories (dashed-bold lines) and the maintenance of gene flow between populations of distinct lineages (GF) are in accordance with a combination of paleogenetic data reported by Krause and colleagues [42] and by Reich and colleagues [44]. According to this scenario, Ceprano would represent one of the latest representatives of the most archaic variant of *H. heidelbergensis* (1) whereas more derived subspecies, respectively, in Europe (2) and in Africa (3), led to the allopatric speciation of *H. neanderthalensis* and *H. sapiens* (both schematically represented in the graph by triangles). Eventually, *H. h. daliensis* (4) would include all the “non-erectus” archaic humans distributed in mainland Asia before the diffusion of *H. sapiens*. Localised interspecific hybridization between *H. heidelbergensis* or *H. neanderthalensis* versus *H. sapiens* is admitted by the model (according to [44–46]). Penecontemporaneous human lineages and/or species—such as *H. erectus* and *H. floresiensis* (compare Figure 1)—are not represented in this diagram.

names—according to the rules of the International Code of Zoological Nomenclature (<http://www.nhm.ac.uk/hosted-sites/iczn/code/>; for a pivotal reference of its application in paleoanthropology, as well as for the use of sub-species, see the seminal paper by Campbell [94])—the most proper denominations for these subspecies respectively should be:

(1) *H. heidelbergensis heidelbergensis* [95]: the ancestral and still largely unknown variety of the species, including the name-bearing type from Mauer (Germany) and other specimens that are either demonstrably archaic or not involved in the respective regional lineages; it would include fossil crania such as Arago, Bodo, Ceprano, and possibly Petralona (for the inclusion in this group of a rather composite fossil record, which combines so far mandibles and crania, see [47]; for a consistent approach to postcranial remains, see [96]); among this sample, Ceprano represents at present the best available expression of the ancestral morphology for this taxon, as far as the braincase districts are concerned;

(2) *H. heidelbergensis steinheimensis* [97]: for the European lineage of the Middle Pleistocene leading to the Neanderthals, including the type specimen from Steinheim (Germany) and other samples such as, most notably, the assemblage from Atapuerca SH [36];

(3) *H. heidelbergensis rhodesiensis* [98]: for the African fossil record of the Middle Pleistocene preceding the appearance of modern humans, including the type specimen from Kabwe (Zambia) and possibly all the late Middle Pleistocene material from various parts of the continent formerly included within the informal group “archaic *H. sapiens*” [99], that is with the exclusion of penecontemporaneous anatomically modern specimens;

(4) *H. heidelbergensis daliensis* [43]: for the Asian non-erectus sample bracketed, at least, between Dali (China, type specimen of this subspecies) and the diminutive, but very informative fossil material from Denisova [42, 44].



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