On the trail of the genus *Homo* between archaic and derived morphologies*

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Summary – *The topic of this review is the evolution of the genus* Homo, *focusing on evolutionary transitions that occurred during the Early and Middle Pleistocene. Two crucial issues are addressed in particular: 1) the emergence in the Early Pleistocene of the archaic variant of Homo that might represent the last common ancestor before the emergence of at least two (more probably three) geographically distinct trajectories; and (2) the evolution of these derived lineages, ultimately leading to the allopatric speciations of the most encephalised species of* Homo: H. neanderthalensis *and* H. sapiens. *In this framework, the time window between 1.0 million years ago (Ma) and 500 thousand years ago (ka) is of crucial importance, since it is probable that a new kind of humanity emerged in this period and then spread across a wide area encompassing Africa and Eurasia. These humans are represented by a number of specimens that are included within the single, polymorphic, and widespread species* H. heidelbergensis. *It is suggested that, in the course of the Middle Pleistocene, this species diversified in a number of incipient species – or subspecies – geographically and phenotypically distinct from one another. The case-study furnished by the calvarium found near Ceprano, in Italy, is of great interest in this regard, since it displays the least derived morphology seen among the hypodigm of* H. heidelbergensis, *and may represent better than other specimens the ancestral morphotype (i.e., the stem subspecies) of this taxon.*

Keywords - *Hominin evolution, Genus* Homo, *Early Pleistocene, Middle Pleistocene, Lower Paleolithic, Cranial morphology,* Homo heidelbergensis, *Subspecies.*

Introduction

During most of the 20th century, scholars interpreting the evolution of the genus *Homo* shared a paradigm implying the existence of a single human species that progressively evolved over the entire Pleistocene. This is known as "the single-species hypothesis" (Weidenreich, 1947; Mayr, 1950), consistent with the gradualist perspective of the "modern synthesis" (Huxley, 1942). According to this model, the current variability of *H. sapiens* was considered to have been the result of small changes occurring through time in local populations of a single and widespread species. The origin of this lineage would have

taken place from the original spread of the genus *Homo*: a phenomenon known as "out-of-Africa 1". The model of progressive change then required the persistence of a single, widely-distributed, and polymorphic humanity throughout most of the Pleistocene. It thus assumed the existence of successive evolutionary stages of an archaic species – usually referred to as *H. erectus* – followed by "grades" of another, more derived species: *i.e.*, *H. sapiens*. In this perspective, *H. erectus* was regarded as the first human species to leave Africa, equipped with a brain of about 1,000 ml and skilled enough to produce the elaborate Acheulean or "Mode 2" (Clark, 1968) Paleolithic stone tools. These were the quasi-modern aptitudes that made these

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humans capable of facing a range of diverse environmental conditions.

Despite regional morphs were identified among either the archaic or the derived species, the focus was on stages/grades instead of clades (Wood & Lonergan, 2008). Thus, assuming that *H. erectus* was present in Asia, Africa, and even Europe, each archaic regional variant was viewed as ultimately moving towards a different "race" among the extant human diversity (compare Coon, 1962). At the same time, the species *H. sapiens* included both recent populations and extinct morphotypes, respectively ascribed to a small number of subspecies, while the adoption of a trinominal nomenclature gave rise to nomina such as *H. sapiens sapiens* and *H. sapiens neanderthalensis* (Mayr, 1950; Campbell, 1965). Another example might be some Middle Pleistocene specimens found in Africa (e.g., Kabwe) and Eurasia (e.g., Petralona, Dali) lumped within *H. sapiens* and often referred to as "archaic *H. sapiens*", according to such a "gradistic" scheme (as in Stringer *et al.,* 1979).

The theory called "multiregional evolution", introduced by M.H. Wolpoff and colleagues in the early '80s (*e.g.*, Wolpoff *et al.*, 1984), may be considered as a recent version of this view. Based on the observation that a certain degree of "regional continuity" characterizes the morphologies of archaic and modern populations within each geographical area (Thorne & Wolpoff, 1981; Wolpoff *et al.*, 1984, 2001; Frayer *et al.*, 1981), this model suggests that the anatomically modern humans of Africa, Asia and Europe emerged from archaic populations that existed in each respective region. At the same time, during their evolution throughout great part of the Pleistocene, all these populations were kept as single species by a significant amount and pervasiveness of gene flow.

A tentative updated scenario

Out of Africa 1

Therefore, according to the evolutionary paradigm of the '40s (Weidenreich, 1947; Mayr, 1950), even popular interpretations of the hominin fossil record implied for decades that *H. erectus* was a widespread species that included a number of archaic-looking and (by contrast) culturally quasi-modern fossil samples, which were considered ancestral in each region to corresponding populations of *H. sapiens*.

However, more recently an increasing body of data suggests a different scenario (Fig. 1). Above all, the evidence from the Georgian site of Dmanisi (Gabunia *et al.*, 2002; Rightmire *et al.*, 2006; Rightmire & Lordkipanidze, 2009) demonstrates that hominins engaged in the first out-of-Africa diffusion were not derived, encephalised, and technologically advanced humans, but were definitely more archaic than previously believed, with a brain just above the threshold of 500-600 ml (maximum encephalic volume of the australopithecines) and a morphology close to the changing definition and hypodigm of *H. habilis* (after Leakey *et al.*, 1964). Driven by ecological, rather than by behavioural or "cultural" motives, these hominins had a tendency to diffuse and to adapt to variable non-tropical environments.

Under this new approach, *H. erectus* is now generally viewed as an Eastern Asian species of *Homo* (*contra* Asfaw *et al.*, 2002; see *e.g.* Manzi *et al.*, 2003), distributed in the island of Java and in Northern China, whereas its African counterparts are considered as a distinct species and referred to as *H. ergaster* (Groves & Mazák, 1975; Wood, 1991). Alternatively, these two geographical variants are grouped together as *H. erectus* sensu lato, while *H. erectus* sensu stricto would be the Asian deme of this a multiregional taxon. The same corpus of data suggests also that the earliest out-of-Africa dispersal would have started well before the appearance of either *H. erectus* sensu stricto, or the Acheulean (which are now regarded as geographically distinct and thus independent phenomena), that is between more than 2,0 and 1,6 Ma.

At the same time, other species have been named and/or old nomina have been reconsidered. These include (ordered according to the respective original denominations): *H. heidelbergensis (1908)*, *H. rhodesiensis (1921)*, *H. pekinensis* (1927), *H. soloensis* (1932), *H. helmei (1935)*,

H. mauritanicus (1954), H. leakeyi (1963), H. rudolfensis (1986), H. antecessor(1997), H. georgicus (2002), H. cepranensis (2003), H. floresiensis (2004). However, many of these taxa are debated and/or are not widely acknowledged. In fact, the most robust scenario is far less speciose than this listing suggests. The identification of a number of different species within the genus *Homo* probably implies an overestimate of interspecific diversity, whereas in many cases this diversity was probably intraspecific (and should be referred to the rank of subspecies; see below). Nevertheless (according, e.g., to the seminal paper by Tattersall, 1986), this speciose scenario confers a more reasonable significance to human varieties that were formerly disguised as variants of *H. erectus* (*sensu lato*), or as members of the informal and confusing entity until recently known as "archaic *H. sapiens*"; and this latter designation is now thankfully disappearing from the literature.

Across Europe

Two distinct waves of immigrants In Europe seem to be recognizable at present, respectively in the late Early (until 780 ka) and in the Middle Pleistocene (after 780 ka). The fossil record documenting the former one of these dispersals is referred – at least in part – to *H. antecessor* (Bermúdez de Castro *et al.*, 1997). Possible representatives of this species have been discovered only in two sites of the Sierra de Atapuerca, near Burgos in Spain (see Fig. 2): in the layer TE9 of the Sima del Elefante, dated to 1,2-1,3 Ma (Carbonell *et al.*, 2008), and in the layer TD6 of the Gran Dolina, dated to more than 780 ka (Carbonell *et al.*, 1995; Bermúdez de Castro *et al.*, 1997). However, a detailed analysis of the morphology of the partial mandible and teeth from Atapuerca TE9 (Bermúdez de Castro *et al.*, 2011) critically reconsidered the putative attribution to *H. antecessor* of this "earliest European", which is not included so far in any named taxon.

The fossil record from Atapuerca bracketed between 1,3 Ma and 780 ka is in association with the Lower Paleolithic so-called Oldowan or "Mode 1" (Clark, 1968). At the same time, Mode 1 assemblages are widely distributed in Mediterranean and continental regions of Europe (Hovers & Braun, 2009). The earliest appearance of any Paleolithic in Europe is recorded by recent findings in Spain (Toro-Moyano *et al.*, 2003), in Southern France (Crochet *et al.*, 2009), and also in Italy, where hominin presence is suggested by the stone tools found at Pirro Nord, near Apricena in Puglia (Arzarello *et al.*, 2007, 2009), in association with a rich paleontological assemblage biostratigraphically referred to a Faunal Unit of the Early Pleistocene (about 1,4 Ma) (Sardella *et al.*, 1998). Also of interest in Italy are sites dated to about 1,0 Ma such as Monte Poggiolo (Peretto *et al.*, 1998) or a number of localities in the Ceprano basin and surroundings that have recently been subject to new excavations and analyses (Segre & Biddittu, 2009). We may add that, between 950 and 700 ka, these humans were capable to adapt to higher latitudes, as demonstrated by sites in Southern England (Parfitt *et al.*, 2010). Nevertheless, it is worth noting that these incursions would have been strongly influenced by ecological conditions and, thus that hominin presence in Western Europe was presumably discontinuous until about 600 ka (Agustí *et al.*, 2009), perhaps in relationship with distinct waves of diffusion.

The major discontinuity was represented by Marine Isotopic Stage (MIS) 16 (see discussion in Manzi *et al.*, 2011), which was one of the most extreme glaciations of the last million years, with an ice sheet extension below 50° latitude in Eastern Europe (Helmke *et al.*, 2003). MIS 16 represented a possible cause of extinction of the earliest Europeans: it is reasonable, in fact, that this climatic collapse created a strong environmental barrier along time, and was probably associated with a population discontinuity at the species level. It might not be by chance that MIS 16 preceded both the appearance of the Acheulean (Mode 2) technology in the continent, and the occurrence of a more abundant fossil record with a diverse morphological appearance if compared to *H. antecessor* and/or to the sample from Dmanisi (see Fig. 2).

This second dispersal into Europe probably occurred after 700-600 ka and was related to
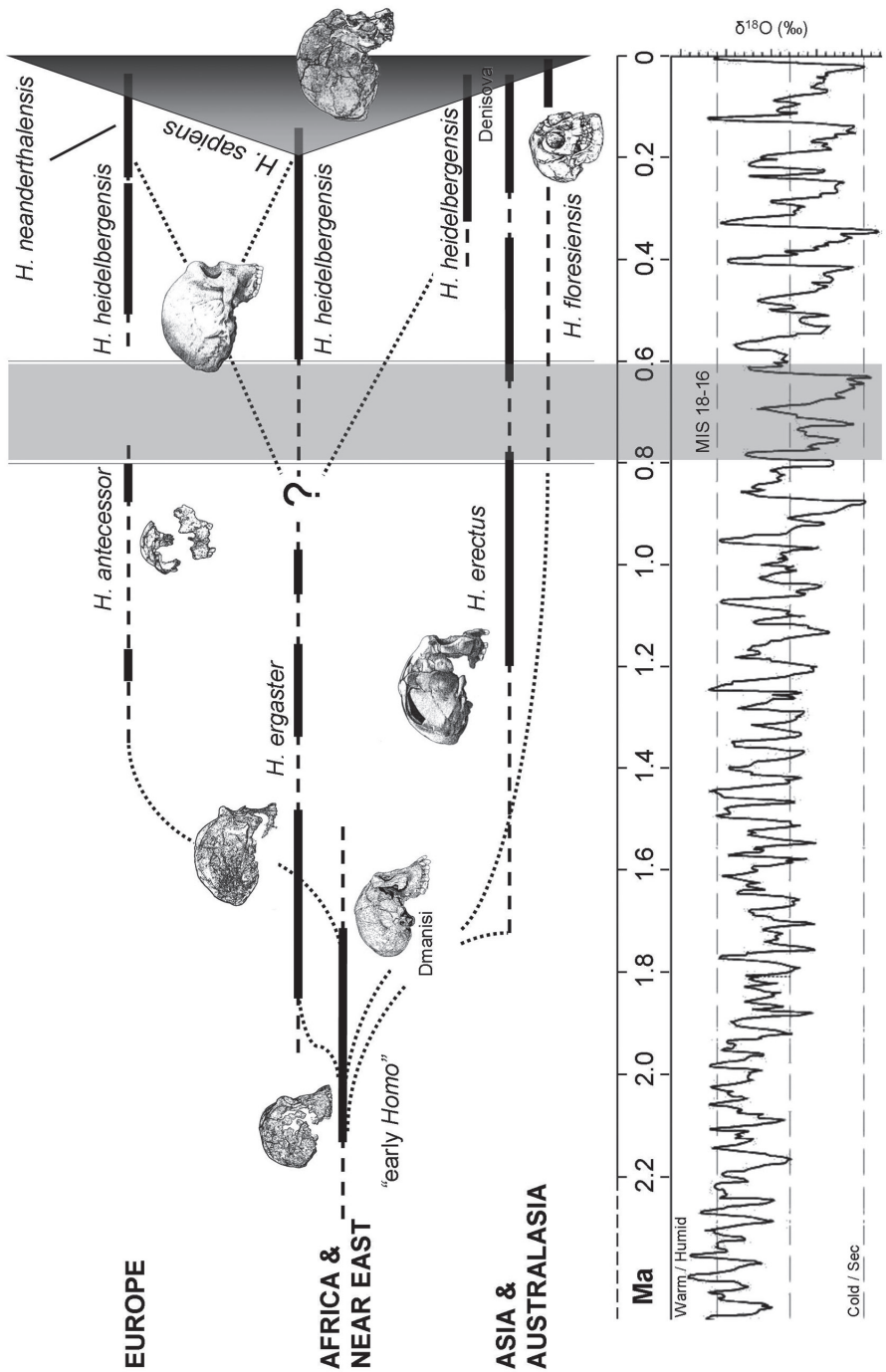
***Fig. 1** - Tentative chronology and topology of the fossil record pertaining to the genus Homo (**bold lines** = hard fossil evidence; dashed lines = inferred hominin occurrence); trajectories of diffusion and/or phylogenetic relationships between a limited number of species are also indicated (dotted lines). It is also reported (below) a curve of climatic variations based on marine isotopic stages, where the **extremely cold/arid period bracketed between MIS 18 and MIS 16 is evidenced**.*

morphologically-derived hominids with clear signs of further encephalization, that are well known from a number of sites. The most notable such assemblage of fossil material is again in the Sierra de Atapuerca (e.g., Arsuaga *et al.*, 1997), namely at the site with the evocative name of Sima de los Huesos (SH): the extraordinarily rich and well preserved human sample, which has been pushed back to about 600 ka (Bischoff *et al.*, 2007). These and a number of other European fossil samples of the Middle Pleistocene (see below) may be regarded as falling within the polymorphic variability of *H. heidelbergensis* (Rightmire, 1998; Mounier *et al.,* 2009, 2011), a species described in Africa and Eurasia that is frequently associated with Mode 2 lower Paleolithic assemblages.

H. antecessor and *H. heidelbergensis* are regarded as competing with each other for the same phylogenetic position, as seen in alternative proposed scenarios of human evolution. *H. antecessor* is claimed by the Spanish workers (after Bermúdez de Castro *et al.*, 1997) as the stem-species that was ancestral to the evolutionary divergence between the evolutionary lineage of the Neanderthals in Europe and to the origin of our species in sub-Saharan Africa. Nonetheless, *H. heidelbergensis* has also been considered as pertinent in the same crucial role (Stringer, 1983; Rightmire, 1996), and this interpretation appears to me more robust at present (e.g., Manzi & Di Vincenzo, 2012).

In a sense, the Sierra de Atapuerca contains evidence that could resolve this ambivalence, since this small karstic hill in Northern Spain includes sites with samples of either *H. antecessor* or *H. heidelbergensis*. It should be remarked that the material from Atapuerca SH (*H.* cf. *heidelbergensis*) is clearly Neanderthal-like, being characterized by a number of features that, later in the Pleistocene, would typify the Neanderthals (Santa Luca, 1978; Dean *et al.*, 1998). From the perspective of published views on Atapuerca SH (Arsuaga *et al.*, 1997; Rak *et al.*, 2011), *H. heidelbergensis* would have the identity of a European regional chronospecies antecedent to *H. neanderthalensis* or would be even part of this taxon. Thus, *H. heidelbergensis* would emerge as

inappropriate to be also ancestral to the African emergence of *H. sapiens*. Nevertheless, there are in Europe other fossil specimens – such as the calvarium from Ceprano in Italy (see Fig. 2), but not only – that are penecontemporaneous with the material from Atapuerca SH, and might represent (far better than the Spanish sample) a possible ancestral morphotype of *H. heidelbergensis* (see below), supporting the alternative hypothesis that this species – taken as a whole, while joining African and Eurasian fossil samples – might represent the evolutionary stem leading to the divergence between Neanderthals and modern humans (compare, e.g., Endicott *et al.*, 2010).

Back to Africa

African hominins dated to around 1,0 Ma – i.e., specimens from sites such as Bouri (Daka), Buia, and Olorgesailie (Fig. 2) – share morphological affinities with *H. ergaster*, as pointed out by Manzi and colleagues (2003), among others. In this perspective, these crania of the late Early Pleistocene are distinct from the African hominins of the Middle Pleistocene – like Bodo, and Kabwe – that are referred to *H. heidelbergensis* (or, alternatively, to *H. rhodesiensis*).

This observation suggests a taxonomic and phylogenetic discontinuity that ranges across the Matuyama-Brunhes boundary (780 ka). Such a phenetic distance between *H. ergaster* (until 900 ka) and *H. heidelbergensis* (after 600 ka) supports, here as in Europe, a distinction at the species level. Might it also signal an allochthonous (non-African) origin of the Mid-Pleistocene taxon? Unfortunately, in sub-Saharan Africa and not only there the period between 900 and 600 ka is very poor in fossil evidence. In addition, representatives of *H. ergaster* are distinct from Mid-Pleistocene fossils either from Europe – including both the Italian calvarium from Ceprano (*contra* Mallegni *et al.*, 2003) and, even more clearly, the assemblage from Atapuerca SH – or mainland Asia, as represented by specimens such as Narmada, Dali, and Jinniushan. These Eurasian samples are in turn also distinguishable from *H. antecessor* in Europe, and from *H. erectus sensu stricto* in the Far East.

Fig. 2 - Geographic distribution of sites with fossil hominins mentioned in the text.

Therefore, although we still do not know where and exactly when, it seems that something happened between about 900 ka and 600 ka that generated a new and more encephalised kind of humanity spreading quite rapidly in Africa and Eurasia, which may be referred to as the single and widely-diffused species *H. heidelbergensis*. These "new" humans appear clearly different from the variable assemblage that derived from the earliest dispersal out of Africa, including *H. ergaster*, *H. antecessor*, *H. erectus* and also, probably, the singular diminutive form referred to as *H. floresiensis* (Brown *et al.*, 2004). At present, however, the chronology, topology, and phylogenetic dynamics related to the rather synchronous appearance of Middle Pleistocene humans that we may refer to *H. heidelbergensis* are still unclear. As a matter of fact, we do not know the provenance of the archaic humans that spread geographically and were ancestral both to Neanderthals and *H. sapiens* (Rightmire, 2008; Hublin, 2009).

Denisova

A possible answer about the last common ancestor of Neanderthal and modern humans comes from the complete mitochondrial DNA (mtDNA) sequence extracted from a human phalanx found at the Denisova cave in the Altai mountains, Southern Siberia (Krause *et al.*, 2010). 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, and contains archaeological assemblages including both Middle and Upper Palaeolithic. By contrast, the mtDNA surprisingly points to humans that were different from both *H. neanderthalensis* and *H. sapiens*, but that shared with them a common ancestor at less than 1,0 Ma (Krause *et al.*, 2010).

As a working hypothesis, this suggests that the Denisova phalanx may represent a still unknown hominin species that originated before the beginning of the Middle Pleistocene, interestingly just

before the appearance of *H. heidelbergensis* in the fossil record.

Researchers have opted to wait for their data to provide a clearer picture before giving this largely hypothetical species a formal name. Nevertheless, it is already possible to speculate that the Denisova hominins was in relation with a "non-*erectus*" occupation of mainland Asia during the Middle Pleistocene. In fact, assuming that *H. erectus* was one of the evolutionary outcomes of the earliest diffusion in Eurasia – and therefore excluding this taxon from the scope of possibilities – we need to look to other humans that were in Asia during the Middle Pleistocene. We should thus focus on specimens, such as Dali and Jinniushan, that in the past have been ascribed to *H. sapiens daliensis* (Wu, 1981) and are currently considered by various authors as representatives of the Easternmost populations of *H. heidelbergensis* (after Rightmire, 1996, 1998). Which raises the question of whether or not it would be appropriate to ascribe the phalanx from Denisova, and its precious molecular content, to a late variant of the same taxon that Dali, Jinniushan, and other "non-*erectus*" specimens from the late Middle Pleistocene belong to.

Further analyses on the Denisova material – including exceptionally preserved nuclear DNA from the phalanx and the discovery of an upper molar – led the same group of researchers to publish additional data (Reich *et al.*, 2010). These new data, based on sequences of nuclear DNA and the morphology of the tooth, confirmed that the Denisova individuals exhibit molecular and dental features that appear "archaic". In contrast, the picture that emerges from the analysis of the nuclear genome suggests that this human group has affinities with the Neanderthals, closer than those expected from the mtDNA. Surprisingly, the scenario that has been suggested according to these new data places the Denisova hominins as a sister group of the 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.*, 2010, p. 1057). However, Reich and colleagues (2010, p. 1057) admit also that "other,

more complex models could explain the data". As a matter of fact, in my view, the occurrence of gene flow across Eurasia, between the ancestors of both Neanderthals and the Denisovan hominins, could be a better explanation of their affinities in nuclear DNA (compare Fig. 5).

Consistently, the observed genetic diversity between Neanderthals and modern humans coalesced at around 500 ka (Green *et al.*, 2008; Briggs *et al.*, 2009; Endicott *et al.*, 2010), substantiating previous conclusions based on morphology and palaeogeography. These suggest isolation and divergence between the European and African lineages during the Middle and the early Late Pleistocene (after Santa Luca, 1978). Indeed, looking at the hypodigm of *H. heidelbergensis* as a whole (compare Fig. 4) it is clear that a considerable amount of variability characterises this species (Mounier, 2009). In other words, we should conclude that populations of *H. heidelbergensis* bore regional features (in Africa, Asia, and Europe respectively) that are referable to a phenomenon known as "isolation by distance" (Wright, 1943). At the same time, considerable phenotypic variation has to be noted even within the European fossil record of the Middle Pleistocene, recently greatly expanded by the revised chronology of the calvarium from Ceprano in Italy (Manzi *et al.*, 2010).

The case-study of Ceprano

A cranium for the earliest Europeans?

At the beginning of the 1990s, a "short chronology" for the earliest inhabitants of Europe was introduced (Roebroeks & van Kolfschoten, 1994), suggesting that no humans were present in Europe before approximately 500 ka. This date was claimed consistent with the chronology of both the oldest human fossil record found in Europe since that time (*e.g.*, Roberts *et al.*, 1994), and the earliest documentation of Acheulean assemblages discovered in various part of the continent (*e.g.*, Piperno *et al.,* 1998). In 1994, however, fossils that were considered older than 700-800 ka, from both Italy (Ceprano, March
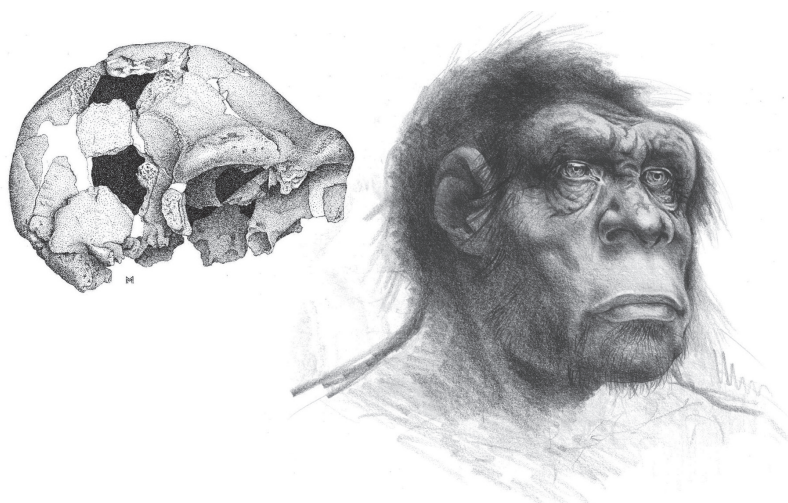
Fig. 3 - Drawing of the Ceprano calvarium compared to a suggestive representation of the human-kind that the Italian fossil might represent (drawings by Maurizio Mei and Carlo Ranzi respectively).

1994; Ascenzi *et al.*, 1996) and Spain (Atapuerca TD6, July 1994; Carbonell *et al.*, 1995), falsified this hypothesis. Thus, for more than a decade the Ceprano calvarium was considered part of the fossil evidence documenting the human presence in Europe before 500 ka.

The Italian specimen (Fig. 3) 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 represented the result of systematic field activities conducted for decades in Southern Lazio by the Italian Institute of Human Palaeontology, and particularly by I Biddittu. On March 13th 1994, during a survey along the trench excavated for a new road, Biddittu found a great number of fragments of a single cranium in the section created by the excavators. All the fragments were then carefully extracted and sieved from the in situ clayey sediments. The reconstruction of the cranium from these pieces required the coordinated efforts of a various experts and, overall, about five years (Ascenzi *et al.*, 1996, 2000; Clarke, 2000).

At the same time, for the purposes of chronological reference, the geologist A.G. Segre suggested a synthetic stratigraphic column based on geo-palaeontological data that were available at a micro-regional scale. This stratigraphy describes two main complexes: the layer where the human calvarium was found belongs to the lower portion of the upper stratigraphic complex, indicating to Segre a tentative age of about 800-900 ka (Ascenzi *et al.*, 1996, 2000) and the archaic features of the calvarium were considered consistent with the various Mode 1 techno-complexes from sites scattered in the Ceprano basin (Segre & Biddittu, 2009), despite the fact that a number of Acheulean assemblages are also well known at Campogrande and in its surroundings.

The muddle in the middle

In this context, a project of surveys and excavations started in 2001 under the direction of I. Biddittu and myself (with the licence of the Soprintendenza Archeologica del Lazio), with a threefold aim: 1) better comprehension of the Pleistocene stratigraphy of the Ceprano basin; 2) definite validation of the available geo-chronological model (Ascenzi *et al.*, 1996, 2000); 3) improvement of the palaeontological and archaeological records.

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 actually more recent than was previously believed, pointing to a time range close to about 400 ka and, more precisely, to the interval at the beginning of MIS 11 bracketed between 430 and 385 ka. This chronology is also consistent with the normal geomagnetic polarity recorded in the area of discovery down to a depth of about 50 metres (Muttoni *et al.*, 2009). These unexpected results, and the consequent new chronology of the fossil specimen in the midpart of the Middle Pleistocene, led us to conclude 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 - appears now tantalizing», pointing out to «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 co-existence of different lineages (with their own respective archaeological traditions) during part of the Middle Pleistocene» (Manzi *et al.,* 2010, p. 584).

This also called for a taxonomic re-evaluation of the Italian specimen. Originally, Ceprano was attributed to "late *H. erectus*" (Ascenzi *et al.*, 1996; Clarke, 2000). Subsequently, two papers criticized the *H. erectus* affinities originally claimed (Ascenzi *et al.*, 2000; Manzi *et al.*, 2001), arguing that less than two-thirds of the character states were in accord (and not always unequivocally) with those commonly encountered in *H. erectus* sensu stricto, while others appeared peculiar or progressive. Further studies included a cladistic approach, with the questionable proposal of a new species name (Mallegni *et al.*, 2003), whereas the CT scanning of the specimen (Bruner & Manzi, 2005) and other phenetic data (Manzi *et al.*, 2003; Manzi, 2004; Bruner & Manzi, 2007) produced additional elements that were useful to better understand the specimen in a comparative framework.

On the whole, these researches largely supported the following conclusions (see, *e.g.*, Manzi *et al.*, 2001). 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 is unfavourably enlarged when Ceprano is added. Second, there are discrete features that detach Ceprano from its claimed "*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 traits, while it shows some affinities with the African penecontemporaneous fossil record that are closer than the affinities it has with its European counterparts. A possible conclusion is that Ceprano represents a mosaic morphological link between the clade composed by the group of species referred to as *H. erectus* sensu lato, on 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 *Homo heidelbergensis/rhodesiensis*» (Bruner & Manzi, 2007, p. 365), the cranial morphology of which was partially lost along the subsequent trajectory of human evolution in Europe, but that was preserved elsewhere (including Africa and, possibly, mainland Asia).

Mounier and colleagues (2011) recently reconsidered the morphology of the Ceprano calvarium in a wide comparative framework, including the fossil record pertaining to *H. heidelbergensis* and related species. This new extended analysis, which combines geometric morphometrics with the evaluation of discrete features, provides robust and independent corroboration to the previous hypothesis and supports the attribution of Ceprano to an archaic variety of *H. heidelbergensis* (see also Manzi, 2011; Manzi & Di Vincenzo, 2012). In conclusion, despite its relatively recent age in the Middle Pleistocene, the Italian specimen may represent the morphology of the as yet undiscovered ancestral stock of the human variability represented in the fossil record of the second part of the Middle Pleistocene from Africa and Eurasia (Fig. 4).
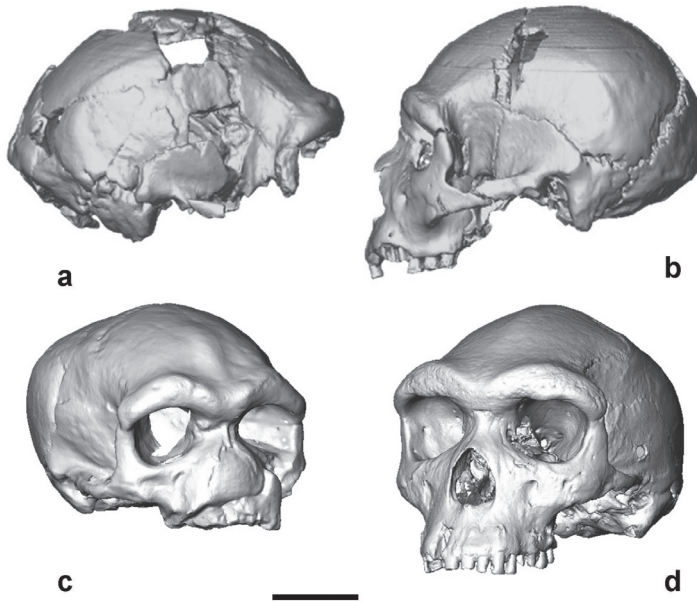
Fig. 4 - Examples of variability in cranial morphology during the second part of the Middle Pleistocene, i.e. roughly between 500 and 150 ka: a – Ceprano (Italy, Europe); b – Atapuerca SH 5 (Spain, Europe); c – Dali (China, Asia); d – Kabwe (Zambia, Africa). Scale bar = 5 cm.

Towards recent Homo

Neanderthals and modern humans

The Ceprano calvarium is thus part of Middle Pleistocene hominins scattered in Europe from northern latitudes (e.g., Swanscombe in England; Mauer, Bilzinsgleben, and Steinheim in Germany; etc.) to the Mediterranean regions (including the large sample from Atapuerca SH in Spain; Arago in Southern France; Petralona in Greece; Venosa and Visogliano in Italy; etc.). As we have seen, this a relatively rich fossil record is considered by many authors to be part of the hypodigm of the species *H. heidelbergensis* (Rightmire, 1998; Mounier *et al.*, 2009), named for the European Mauer mandible (Schoetensack, 1908). In addition, data cited in this review suggest that this Mid-Pleistocene fossil record represents the dispersal in Western Eurasia of hominins bearing the Mode 2 techno-complexes. Their exact place of origin is still not clear, though it may be assumed that they ultimately emerged from Africa (Asfaw *et al.*, 1992; Krause *et al.*, 2010) or from the Near East (Dennel *et al.*, 2011; Bermúdez de Castro & Martinon-Torres, 2012). We also already stressed in this paper that these Acheulean-bearing humans exhibit a clear discontinuity in morphology with more archaic humans from Europe (i.e., *H. antecessor*) and elsewhere (i.e., *H. ergaster* and *H. erectus*).

Subsequent hominin evolution in Europe during the Middle Pleistocene agrees with a persistent geographic isolation of human populations to the north of the Mediterranean: a scenario that is supported both morphologically and genetically (Stringer, 1974; Santa Luca, 1978; Green *et al.*, 2008, 2010; Weaver *et al.*, 2008). In sync with this pattern of evolution, the so-called "accretion model" (Dean *et al.*, 1998; Hublin, 2000, 2009) proposes that fossil samples are characterised by an increase of Neanderthal features, in possible relationship with the dramatic climatic swings bracketed between MIS 16 and MIS 2. These glaciations might have
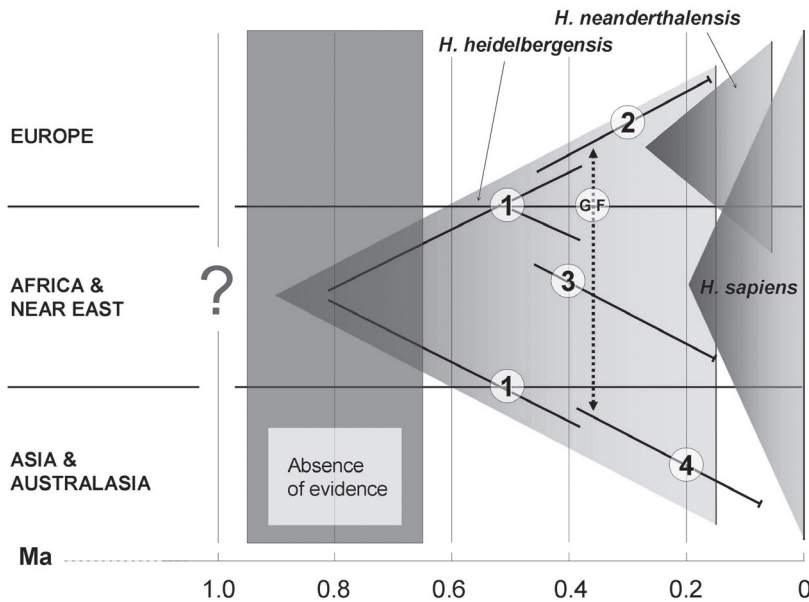
Fig. 5 - **H. heidelbergensis** *and its putative subspecies in time and space, as suggested in this paper (see also Manzi, 2011; Manzi & Di Vincenzo, 2012): 1)* **H. h. heidelbergensis; 2)** **H. h. steinheimensis;** *3)* **H. h. rhodesiensis; 4)** **H. h. daliensis.** *The main evolutionary trajectories (dashed bold lines) and the maintenance of gene flow between lineages (GF) are in accordance with a combination between the fossil evidence (compare text for references) and genetic data (see in particular Krause et al., 2010; Reich et al., 2010). The origin of both* **H. neanderthalensis** *and* **H. sapiens** *are schematically represented as allopatric speciations emerging from the variability of* **H. heidelbergensis,** *while other penecontemporaneous species (e.g.,* **H. erectus***) are not represented in this diagram. Localised interspecific hybridizations between the "archaic" (***H. heidelbergensis,** **H. neanderthalensis***) and the modern species (***H. sapiens***) are also admitted by this model (according to Reich et al., 2010; Green et al., 2010; Voisin 2006). The color version of this figure is available at the JASs website.*

produced recurrent demographic crashes and population bottlenecks, favouring either genetic drift or adaptation to cold climatic conditions. Eventually, at the boundary between the Middle and Late Pleistocene, the European evolutionary lineage is represented by *H. neanderthalensis* only.

Nevertheless, our growing knowledge of the European fossil record does not completely support a linear and gradual process of change (Stringer & Hublin, 1999; Hawks & Wolpoff, 2001; Tattersall & Schwartz, 2006). For instance, endocranial metric variation fails to demonstrate the occurrence of sequential discrete steps along this hypothetical anagenetic process (Bruner *et*

al., 2006). Moreover, the Neanderthals – even in their earliest representatives, such as those from Saccopastore (Bruner & Manzi, 2008) – seem to be characterized by a well-defined brain morphology, emphasizing the phylogenetic independence of *H. neanderthalensis* from *H. heidelbergensis*. This suggests a fairly sharp distinction between two different chronospecies, instead of a gradual process of change. The speciation probably occurred towards the end of the Middle Pleistocene, consistent with palaeogenetic data that support a speciation event around 250 ka (Green *et al.*, 2008; Briggs *et al.*, 2009), hence around the end of the cold isotopic stage MIS 7.

It is reasonable that similar (although not identical) regional patterns of evolution occurred among the populations of _H. heidelbergensis_ that dwelled both in Africa and in Asia during the Middle Pleistocene. The emergence of _H. sapiens_ at about 200 ka in Africa (_e.g._, Stringer, 2002) must be viewed in this framework. However, in my view the pattern in this particular case was peculiar in terms of agency. Looking comparatively at the distinction between Neanderthals and modern humans, various scholars have claimed that the allopatric speciations involved in generating the phenotypic and genetic diversity between these two species of the genus _Homo_ suggests crucial differences in their respective ontogenetic processes (Manzi _et al._, 2000; Ponce de León & Zollikofer, 2001; Ramirez Rozzi & Bermúdez de Castro, 2004). Moreover, although similar trends of encephalisation quantitatively characterize the two derived morphologies, they actually diverge in shape. For while the Neanderthal cranium combines a fundamentally archaic shape of the vault with enlarged brain dimensions, the modern human architecture appears to have been completely redesigned in terms of "globularity" (Lieberman _et al._, 2002). It may be shown, for instance, that while based on a single allometric trend, the Neanderthals share and endocranial model with more archaic humans; the modern range of variability by contrast implies an unusual morphological pattern, with an increased degree of parietal development (Bruner _et al._, 2003). In this light, while a certain level of "allometric stasis" occurred during the evolution of the genus _Homo_, the transition to the new phenotypic and ontogenetic equilibrium associated with the emergence of _H. sapiens_ represents an exception that appears as a sharp disruption of the pattern of evolution of the genus _Homo_ as a whole.

The stem and some incipient species

We have observed that something crucial for the evolution of the genus _Homo_ happened around the beginning of the Middle Pleistocene, between say 900 and 600 ka. Looking at the fossil record in Africa and Eurasia, it appears that differences exist between the late representatives of earlier-established variants of the genus _Homo_ (_e.g._, _H. ergaster, H. erectus, H. antecessor_) on the one hand, and _H. heidelbergensis_, viewed as a widely-diffused and more derived species, on the other.

We noted also that one single specimen among the potential hypodigm of _H. heidelbergensis_ – the calvarium from Ceprano – is sufficiently morphologically archaic, as well as it displays a unique combination of features, to represent the ancestral morphotype of this species. Moreover, it should be stressed that the hypodigm of _H. heidelbergensis_ shows a considerable amount of variability within which regional features may be recognised (Mounier _et al._, 2011), while phenotypic variations are observed even locally. This supports the conclusion that Ceprano best represents among known fossil specimens a possible ancestral stock of _H. heidelbergensis_, close in time to the evolutionary divergence between Neanderthals and modern humans (Endicott _et al._, 2010).

In sum, combining the various elements mentioned in this brief overview, _H. heidelbergensis_ may be considered as a single taxon (Fig. 5) that was both geographically widespread and morphologically diversified. However, given the observed internal diversity of this species, it may be useful to make further distinctions at the sub-specific level, reflecting also the possibility of inbreeding within different demes. I suggest, therefore, that it is appropriate to introduce a trinominal nomenclature for this species (compare Manzi 2011; Manzi & Di Vincenzo, 2012). According to Mayr (1942, p. 155): "every species that developed through geographic speciation had to pass through the subspecies stage." _H. heidelbergensis_ clearly appears to include regional incipient species, something that anticipates the allopatric speciations of _H. neanderthalensis_ (in Europe) and of _H. sapiens_ (in Africa). From this perspective, the use of sub-specific ranks within _H. heidelbergensis_ appears mandated and useful.

As indicated in the schematic representation reported in Figure 5, I propose to divide _H. heidelbergensis_, the species ancestral to both Neanderthals and modern humans (plus the

"Denisovans"; Reich *et al.*, 2010), into a stem variety and other geographically distinct subspecies. Using names already available according to the rules of the International Code of Zoological Nomenclature (see http://www.nhm.ac.uk/hosted-sites/iczn/code), the proper denominations for these subspecies are:

- *H. heidelbergensis heidelbergensis* (Schoetensack, 1908) – the ancestral and still largely unknown variety of the species, represented by the name-bearing type from Mauer and other specimens that are either demonstrably archaic, or not clearly involved in the respective regional lineages. These would include fossil crania such as Arago and Ceprano in Europe, as well as Bodo in Africa, and possibly Hexian in Asia (for an approach based principally on mandibles and crania see Mounier, 2009; for a consistent approach to postcranial remains see Carretero and co-workers, 2009). Among the sample, Ceprano represents at present the best available expression of the possible ancestral morphology for this stem subspecies.
- *H. heidelbergensis steinheimensis* (Berckhemer, 1936) – for the European lineage of the Middle Pleistocene leading to the Neanderthals, including the type specimen from Steinheim, other crania such as Petralona, Reilingen, Swanscombe, and, most notably, the tantalizing assemblage from Atapuerca SH (Arsuaga *et al.*, 1997).
- *H. heidelbergensis rhodesiensis* (Woodward, 1921) – for African hominin fossils of the Middle Pleistocene preceding the appearance of modern humans, including the type specimen from Kabwe and possibly all the late Middle Pleistocene material from various part of the continent formerly included within the informal group "archaic *H. sapiens*" (Bräuer, 1984), such as Djebel Irhoud, Florisbad, Eliye Springs (Turkana), Ngaloba (Laetoli), and Omo Kibish II.
- *H. heidelbergensis daliensis* (Wu, 1981) – for the Asian non-*erectus* hominin sample that lies temporally between Dali (China,

type specimen of this subspecies) and the meagre, but very informative material from Denisova; thus, the sample includes also Jinniushan and Narmada.

Acknowledgements

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