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Homo heidelbergensis as the Middle Pleistocene common ancestor of Denisovans, Neanderthals and modern humans

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ABSTRACT - *Homo sapiens (H. sapiens)* originated as a species in Africa during the late Middle Pleistocene (MP). Around the same time, Neanderthals (*H. neanderthalensis*) emerged in Europe while Denisovans emerged in Asia; in fact, although fossil remains attributed to the so-called Denisovans are still poorly known, ancient DNA data collected in the last decades suggest that they also originated in the MP and were widespread in mainland Asia. These findings indicate that all three of these alleged species share a last common ancestor (LCA) and the same genetic coalescence. This common origin occurred at the onset of the MP, with paleogenetic estimates placing such an event approximately between 1.0 and 0.5 million years ago. Subsequently, during the second half of the MP, the fossil record across Africa and Eurasia exhibits significant variability. Due to the abrupt climatic changes recurring during the MP, this variability can be attributed to local adaptations and/or genetic drift, with the differential survival and extinction of evolutionary lineages. Given this scenario, proper taxonomical identification of the LCA is highly problematic and debated among scholars, leading to the iconic expression "muddle in the middle". We suggest that the LCA should be identified in a single polymorphic species, whose name should be *H. heidelbergensis* (given its taxonomic priority) and whose populations have become progressively isolated and differentiated due to climatic and environmental factors. Over time, these different demes (or subspecies), would have developed distinct characteristics and adaptations, leading to local speciation events (speciation in allopatry). Particularly, the transition in Europe from *H. heidelbergensis* to *H. neanderthalensis* is exemplified by some fossil specimens, such as those discovered in Central Italy (Latium) and including the significant fragment of a parietal bone found in May 1983 at the site of Casal de' Pazzi (Aniene Valley), within the present-day city of Rome.

Keywords: Human evolution; *Homo heidelbergensis*; Last common ancestor; Middle Pleistocene; Africa; Western Eurasia; Eastern Eurasia.

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1. AN UNRESOLVED DEBATE

The Middle Pleistocene (MP) or Chibanian - which occurred between 770 and 126 thousand years before the present, or ka (Cohen et al., 2020) - holds significant importance in Earth's recent history, particularly in concerning to human evolution. It is during this period that the origins of modern humans (*H. sapiens*) in Africa, Neanderthals (*H. neanderthalensis*) in Europe, and the so-called "Denisovans" in mainland Asia can be traced.

However, the MP also saw the persistence of hominin species with more primitive features, including *H. erectus* (Dubois, 1893) in Southeast Asia (Indochina and Indonesia), *H. naledi* (Berger et al., 2015) in southern Africa, and *H. floresiensis* (Brown et al., 2004) on the island of Flores (Sunda). We may also consider *H. antecessor* (Carbonell et al., 1995), in Spain, whose remains are dated just before the beginning of the MP, and species of more uncertain identity such as *H. luzonensis* (Détroit et al., 2019) in the Philippines.

Nonetheless, the MP is primarily characterized by the presence of human populations that cannot be attributed to any of these aforementioned species. In the past, these populations were labeled as ambiguous "archaic" variants of *H. sapiens*. However, in recent decades (following authors such as Stringer, 1983, and Rightmire, 1996, 1998), these populations have been referred to as *H. heidelbergensis* (Shoetensack, 1908), seen as a single polymorphic species. Nevertheless, various alternative designations were proposed during the 20th century and are still occasionally used today, including *H. rhodesiensis* (Woodward, 1921), *H. helmei* (Dreyer, 1935), *H. steinheimensis* (Berckhemer, 1936), *H. (Atlanthropus) mauritanicus* (Arambourg, 1955), *H. (sapiens) daliensis* (Wu, 1981), and so on.

Overall, the MP represents a period marked by significant transitions from archaic morphologies associated with *H. ergaster/erectus* (*sensu lato*) to more derived human species, each with distinct characteristics. These species share novel morphological features such as an increased expansion of the brain volume, associated with new technologies of the Paleolithic (*e.g.*, the Levallois technique), significant changes in human behavior (*e.g.*, the regular use of fire and the occurrence of more complex settlements), as well as in the cognitive faculties that can be inferred from the archaeological and paleoneurological evidence (*e.g.,* Melchionna et al., 2020).

The increasing complexity observed in terms of evolution, taxonomy, morphology, and behavior can be attributed to ecological and environmental factors. Toward the end of the Lower Pleistocene, there was a heightened climatic instability on a global scale leading to the so-called "Early to Middle Pleistocene transition", characterized by a shift in climatic cycles from approximately 40,000 to 100,000 years (Head and Gibbard, 2005; Clark et al., 2006). These cycles exhibited more pronounced fluctuations between hot-humid phases (temperate in the north) and arid-cold phases (glacial in the north). Consequently, the MP was characterized by a high degree of environmental heterogeneity, which exerted a significant influence on the evolution of ecosystems, biotic communities, human populations, and their evolutionary history.

2. GENERAL ASPECTS

The oldest available human paleogenetic sequences to date originate from the MP. These DNA sequences, encompassing both mitochondrial (mtDNA) and nuclear (nDNA) components of the human genome, were extracted from fossils dating back approximately 430 ka, found in the Sima de los Huesos deep cave in the Sierra de Atapuerca, Spain (Meyer et al., 2014, 2016). These genetic sequences, combined with similar data from an increasing number of Neanderthal and Denisovan specimens (Reich et al., 2010; Slon et al., 2018), along with our understanding of the genetic variability within *H. sapiens* (Reich et al., 2011; Vernot et al., 2016; Massilani et al., 2020), have provided a paleogenetic framework. A similar scenario must be considered alongside morphological evidence from the fossil record and archaeological data, to gain insights into the identities of Denisovans, Neanderthals, and Modern Humans, including their phylogenetic relationships when viewed as originating from a common ancestral genetic pool.

It becomes thus possible to establish the chronology of coalescence between distinct evolutionary lineages, marking the beginning of their respective evolutionary divergence and the topology of the phylogenetic tree. It is important to note that these estimates should not be confused with speciation events, which may occur later and under allopatric conditions. Instead, these estimates indicate when evolutionary lineages start to diverge from the variability internal to an ancestral taxon or "last common ancestor" (LCA). Consequently, the appearance of new species, ultimately as a substructure of a monophyletic group, occurs with a tempo and mode that are not easily discernible looking at the fossil record alone (Buck and Stringer, 2014). Therefore, distinguishing clear boundaries between ancestral and derived species often proves difficult. However, in our view, it is important to emphasize that cladogenetic speciation events within a monophyletic group do not correspond (as in the phylogenetic species concept) to the onset of phylogenetic divergence within the ancestral species, but rather to subsequent significant morphological (and even behavioral) changes.

According to available data, the onset of the separation between our lineage and that of the Neanderthals is estimated to have occurred around 500 ka (765-550 ka based on nDNA, Prüfer et al., 2014; 468-219 ka based on mtDNA, Posth et al., 2017). Similarly, the Denisovan lineage diverges from the other two lineages by approximately 600 ka: namely, such a split occurred well before this date, according to the analysis of mtDNA and the Y chromosome (Post et al., 2017; Petret al., 2020) or after this date based on autosomal nDNA (Prüfer et al., 2014; Meyer et al., 2016). Consequently, it is reasonable to suppose that from an ancestral variability, lacking distinct derived traits before around 600 ka, divergent phyletic lineages originated and acquired derived features over time, distinguishing themselves from both LCA and each other. These lineages differentiated respectively in mainland Asia (Denisovans), Europe (Neanderthals), and Africa (modern humans).

This implies an evolutionary scenario that should foresee the following points:

1. Intraspecific differentiation (within the LCA's variability) occurring between approximately 600 ka and 300 ka, which led to the characterization of lineages (paleodemes or subspecies; Manzi, 2016) that were geographically separated, despite still belonging (biologically and taxonomically) to the ancestral (stem) species, which evolutionary originated before 600 ka.
2. Subsequent speciation events (after 300 ka), in which the descending new species, as part of the same monophyletic group, can be defined based on derived genetic, morphological, and behavioral traits (apomorphies).

This is indeed what we observe in the human fossil record of the MP in Africa, as well as in Eastern and Western Eurasia, regarding human morphotypes that cannot be attributed to the variability of other more archaic species, such as *H. ergaster*, *H. erectus, H. naledi*, and *H. floresiensis*. However, there is currently an intense and unresolved debate concerning i) the evolutionary modalities that led to the speciation events; ii) the taxonomic status of many fossil specimens in Africa and Eurasia displaying features that are "mixed" or not "fully" derived; iii) the taxonomic identification of the LCA from which Denisovans, Neanderthals, and modern humans ultimately originated.

Regarding this last point, the LCA has been identified as *H. heidelbergensis* (Stringer, 1983; Rightmire, 1996, 1998; Mounier et al., 2009; but *contra* Stringer, 2018; Harvati and Reyes-Centeno, 2022). This is the binomial name that takes priority over other *nomina*, as it was attributed in 1908 to the Mauer mandible (Shoetensack, 1908), discovered the previous year not far from Heidelberg in Germany. Any hypodigm of fossil specimens that include the Mauer mandible must necessarily be referred to as *H. heidelbergensis*. Nonetheless, this taxon exhibits significant morphological (and potentially genetic) variability and has a wide geographical distribution spanning Africa and Eurasia. It existed for a considerable period within the MP: *i.e.*, between approximately 900 and 300 ka (Hu et al., 2023).

A process of geographical expansion would be attributable to such a new species (Profico et al., 2016). This dispersal led to the spread of populations of this species across Africa and Eurasia. They were small groups of hunter-gatherers - *i.e.*, "band" or small kin groups (*e.g.*, Zatrev, 2014) - equipped with technologies of the Lower Paleolithic or Mode 2 (the Acheulean; Moncel et al., 2020) that appeared in Africa before 1,500 ka. In some areas (for instance in Europe) these "new" humans would have substantially replaced populations and technologies of the Lower Paleolithic or Mode 1 (Oldowan; Carbonell et al., 1995, 2008). From this perspective, *H. heidelbergensis* would therefore be an Afro-Eurasian species that originates from the variability of *H. ergaster* (the African variant of *H. erectus sensu lato*, Groves and Mazak, 1975), at the end of the Lower Pleistocene, following the model introduced by P. Rightmire in 1996 (Fig. 1).

However, several scholars dispute this interpretation (Stinger, 2018; Bergström et al., 2021), claiming that *H. heidelbergensis* (defined as above) would be an excessively variable *taxon* and that the populations following the coalescence events were phyletic lineages that were sufficiently derived to be ascribed to distinct species. This view implies an early differentiation of the evolutionary lines from the LCA, which should have been more ancient than the fossil record currently ascribed to *H. heidelbergensis*. This alternative LCA is identified by some researchers in *H. antecessor* - a species that is represented only in Europe, by the sample of about 800 ka from a single site of the Sierra de Atapuerca, in Spain (Gran Dolina, Arsuaga et al., 1999) - mainly according to the modern-like conformation of the infraorbital (maxillary) region of a juvenile specimen.

The existing contrast among scholars is particularly evident in the interpretation of the European fossil record in relation to the evolutionary emergence of Neanderthal morphological features. However, the discussion has expanded in recent years to include the interpretation of the Denisovans in Asia (Ni et al., 2021; Ji et al., 2021) and the evolutionary modes by which our species emerged from the African variability of the MP (Hublin et al., 2017; Bergström et al., 2021; Meneganzin et al., 2022).

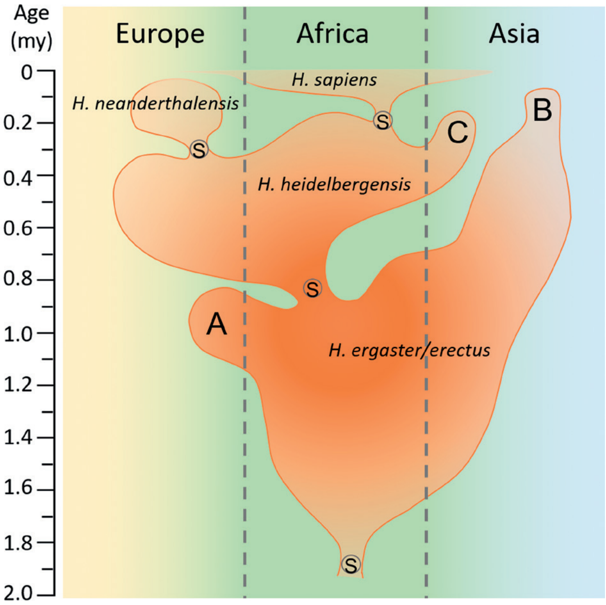

Fig. 1 - Redrawing of the diagram by G. Philip Rightmire (1996) representing the evolution of the genus *Homo* during the Pleistocene. It has been graphically adapted here, with the insertion of letters, aimed at incorporating new discoveries or updating the Rightmire's original diagram. Namely: A) early populations of *Homo* in Western Europe (Atapuerca Trinchera Elefante and Gran Dolina, including *H. antecessor*); B) recent dates for the last occurrence of *H. erectus* in Java (Ngandong) and for *H. floresiensis* in the island of Flores (Liang Bua); C) *H. heidelbergensis* in mainland Asian, along with the identification of the so-called Denisovans; (S) indicates alleged speciation events as in the Rightmire's original diagram.

3. THE FOSSIL RECORD

3.1. AFRICA, BEFORE AND AFTER THE LCA

There is broad consensus among scholars - except for different interpretations of the modalities of the evolutionary pattern (see, *e.g.*, Scerri et al., 2018, *vs* Meneganzin et al., 2022) - that Africa was the continent of origin of our species during the late MP, starting from the previous variability attributed to *H. heidelbergensis* (giving to this *taxon* the already defined meaning of LCA). It is also probable that Africa was the continent where the LCA could have originated (Mounier and Caparros, 2015; Mounier and Mirazón Lahr, 2016; Profico et al., 2016; Hu et al., 2023).

The origin of the LCA would have occurred therefore in Africa, before its diffusion in Eurasia in one or more waves, which probably began in relation to climatic events that led, in the tropical belt, to an alternation between humidity and aridity, with consequent phases of habitat fragmentation. This led to population isolation and, therefore, offered a greater probability of macro-evolutionary events.

In this context, if we examine the paleoanthropological record in Africa throughout the entire Pleistocene, we notice a gap in the fossil record corresponding to the interval between approximately 900 and about 600 ka (Profico et al., 2016; Hu et al., 2023). As a matter of fact, the archaic morphologies of uncertain taxonomic affinity or possibly attributable to late representatives of the species *H. ergaster* - such as Olduvai (OH12) in Tanzania (Antón, 2004), Olorgesailie in Kenya (Potts et al., 2004), Daka in Ethiopia (Asfaw et al., 2002), Buia in Eritrea (Macchiarelli et al., 2004) - suddenly disappeared around one million years ago, if we disregard the later occurrence of *H. naledi*, whose representatives are dated to about 300 ka and show some affinities with the African samples of the Early Pleistocene.

After 600 ka, the human fossil record becomes relatively abundant again, with a series of specimens - such as those from Bodo in Ethiopia, Ndutu in Tanzania, Kabwe in Zambia (also known as Broken Hill, recently dated to around 300 ka, Grün et al., 2020), Saldanha in South Africa - that exhibit more derived features, including average brain volumes of 1,200 ml, a more arched frontal profile, a typical supraorbital torus morphology, etc. These morphologies, combining plesiomorphic (primitive) and apomorphic (derived) features, appear to be primarily distributed in southeastern Africa, but the mandibles from Tighenif (Ternifine, Mounier et al., 2009) in Algeria should also be considered. However, this fossil record can be attributed to the taxon with priority of nomenclature, namely *H. heidelbergensis* (Shoetensack, 1908), even though other taxonomic identities have been proposed over time: *H. rhodesiensis* (Woodward, 1921), *H. saldanensis* (Drennan, 1955), *H. (Atlanthropus) mauritanicus* or "archaic" *H. sapiens* (Arambourg, 1955), and *H. bodoensis* (Roksandic et al., 2021, although this recent proposal is redundant, as stated for instance by Delson and Stringer, 2022).

Subsequently, when we approach 300 ka, more derived morphologies are found, with greater brain volumes and smaller sizes of the teeth and the face. These also assume a modern physiognomy, including the reduction of the supraorbital torus. The African finds of this phase are attributed by some authors (Lahr and Foley, 1998; McBrearty and Brooks, 2000) to yet another species: *H. helmei*, from the name attributed to the partial skull of Florisbad in South Africa, which is joined by the fossil finds Omo-Kibish 2, Eliye Spring and Ngaloba in East Africa, or by those from Jebel Irhoud in Morocco (Bräuer, 2012; Bruner and Pearson, 2013). In this phase, a significant change is also behavioral, as these new forms are associated with a more complex lithic technology, which includes elements of predetermination of the shape of the artifacts and extensive working on flakes: novelties that together characterize the Middle Paleolithic or Mode 3, in Eurasia, called in Africa "Middle Stone Age" (Foley and Lahr, 1997).

Due to the increase in derived traits that they share with *H. sapiens*, these recent findings are currently at the center of the debate regarding the timing and mode of the origin of our species (Hublin et al., 2017; Scerri et al., 2018; Bergström et al., 2021; Meneganzin et al., 2022). However, in these specimens, modern anatomical characteristics (especially in the teeth and face) are combined with the retention of more archaic features, particularly the elongated shape of the cranial vault in the anteroposterior direction (Bruner and Pearson, 2013). Conversely, a globular neurocranium and other more detailed features that are typical of *H. sapiens*, such as a forward protruding chin, only appear in fossil specimens dated to approximately 200 ka (between 230 and 160 ka according to the latest dating, Vidal et al., 2022), such as the crania of Omo-Kibish 1 and Herto, both in Ethiopia, or the more recent and fragmentary ones from Border Cave and Klasies River Mouth in South Africa.

According to some authors (Meneganzin et al., 2022), the acquisition of these characteristics - particularly the cranial globularity, which is associated with a reorganization of the brain, with probable new cognitive faculties, together with a new pattern of growth and development especially in the perinatal age (Bruner et al., 2003; Manzi, 2003; Gunz et al., 2010) - would mark the speciation event (cladogenetic and allopatric) of *H. sapiens*, which occurred around 200 ka in a small, isolated population in center-southern or eastern Africa (Chan et al., 2019; Meneganzin et al., 2022).

Other scholars instead believe that, as in a sort of network of genetic relationships and through an anagenetic (univocal and gradual) evolutionary process, many African populations (if not all) would have contributed to the emergence of *H. sapiens*. The phenomenon - known as the "pan-African" hypothesis for the origin of modern humans - would have already been triggered before 300 ka (Scerri et al., 2018; Mounier and Mirazón Lahr, 2019). It would see in specimens such as the Moroccan Jebel Irhoud (Hublin et al., 2017) the earliest representative of the new species, viewed as the most ancient manifestations that precede the achievement of fully modern humans (Fig. 2).

3.2. ASIA (EASTERN EURASIA)

Since the discovery in the early 1890s in Java, Indonesia, of the first fossil remains by Eugène Dubois (who named them *Pithecanthropus erectus*; Dubois, 1893), it was believed that *H. erectus* was the only human species represented in Asia during the Pleistocene, before the appearance - or, rather, the arrival - of *H. sapiens*.

For a large part of the 20th century, it was also believed that *H. erectus* was a widely distributed taxon that would have given rise to the present-day variability of *H. sapiens*, evolving in different geographical contexts in Asia, Europe, and Africa through parallel trajectories. This was the so-called "candelabra model" suggested

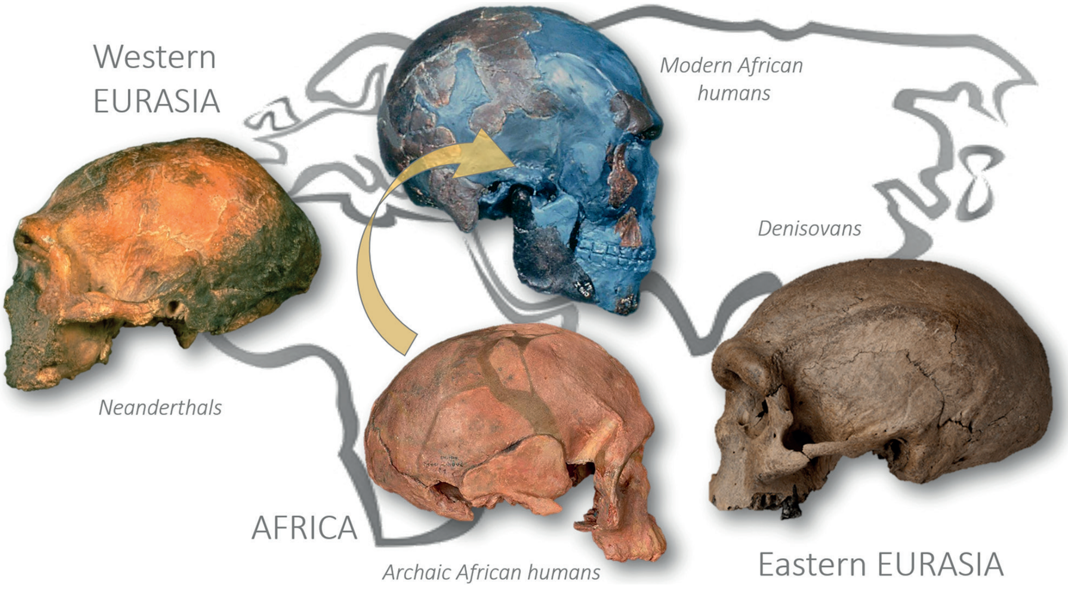

Fig. 2 - During the Middle to Late Pleistocene, both in Africa and Eurasia, variability in facial and dental features is observed (e.g., Neanderthal-like in Europe and modern-like in Africa), combined with a shared cranial morphology characterized by flat and antero-posteriorly elongated cranial vaults. Given this framework, in Africa, from specimens characterized by an apomorphic face and a plesiomorphic vault (such as in Jebel Irhoud 1), *H. sapiens* originated more than 200 ka, with the appearance of a fully modern globular cranial morphology and a mandible with a protruding chin. Images taken from Day and Stringer (1991), Ni et al. (2012), Laboratory of Anthropology and Bioarchaeology of the Sapienza University of Rome, Italy.

by Franz Weidenreich (*e.g.*, 1946) and later adopted by various researchers (Caspari and Wolpoff, 1996). Today, this polycentric perspective on the origins of present human variability -reformulated in the early 1980s as "multiregional evolution", or MRE, which implies the significant contribution of gene flow between populations, maintaining a single evolving species across a pluricontinental scenario (Frayer et al., 1993) - has been abandoned in favor of a different interpretation of the African emergence of *H. sapiens* (see above), which appears more consistent with available fossil and paleogenetic data: the so-called "recent African origin" or RAO (Stringer and Andrews, 1988; Stringer, 2022).

The RAO model suggests that even in Asia there would have been the replacement of archaic humans, all attributable to previous out-of-Africa dispersals that occurred during the Pleistocene. The oldest of these geographical dispersals could have led to the appearance of morphologically archaic taxa such as *H. floresiensis* (Brown et al., 2004) - endemic to the Indonesian island of Flores, beyond the Wallace's biogeographic line - that became extinct in the Late Pleistocene.

The presence of *H. erectus (sensu stricto)* in the Far East is documented in a geographically extensive scenario east of the Himalayas. Fossils with morphology attributable to this species have been found during the MP in Chinese sites such as Zhoukoudian, Yunxian, Chenjiavo, Nanjing, and Yiyuan, as well as in Indonesia (Etler, 1996), specifically on the island of Java, with both older chronologies (Sangiran and Trinil, from the Lower Pleistocene) and more recent ones (Sambungmacan, Ngawi, Ngandong, in the late MP, Rizal et al., 2020). Unlike what happens in Africa with *H. ergaster*, the remains of *H. erectus* in Asia are not associated with lithic assemblages of the Lower Paleolithic of Mode 2. The diffusion of the Acheulean in the Asian continent is poor (Yamei et al., 2000) and can be mainly attributable to fossil human samples that appear in the fossil record of continental Asia starting from approximately 400 ka. These samples show morphological affinities with the hypodigm of *H. heidelbergensis* from Africa and Europe. This new type of Asian inhabitants would have also spread in present-day China and neighboring areas, effectively replacing the populations of *H. erectus* that occupied this vast region. At the same time, the Indonesian variety of *H. erectus* would have continued to survive in Southeast Asia until approximately 100,000 years ago (Rizal et al., 2020), exhibiting characteristics of endemism in the late fossil record from Java.

Specimens possibly belonging *to H. heidelbergensis* are those from sites such as Dali, Chaoxian, Jinniushan, and Harbin. Although sometimes referred to as distinct taxa, such as *H. (sapiens) daliensis* (Wu, 1981) or *H. longi* (Ni et al., 2021; Ji et al., 2021), these finds can be traced back to the pluricontinental variability of *H. heidelbergensis*, being ancestral to the Denisovans, thus following (at least in part) an evolutionary scenario similar to that already described for the contemporaneous fossil record from Africa (leading to *H. sapiens*) and to what we will see in Europe (leading to *H. neanderthalensis*).

At present, proper Denisovan specimens - very fragmentary and partial remains, indeed, but very rich in ancient DNA - are known only from the Denisova cave (in the Altai mountains, not far from the border between Siberia and Mongolia), except for a mandible dated 160,000 years ago from Xihae, in the plateau of Tibet and other sparse dental pieces of evidence (Krause et al., 2010; Slon et al., 2018; Chen et al., 2019; Demeter et al., 2022). Despite this, genetic analyses have revealed that genetic introgressions of Denisovan origin are more pronounced in current human populations of Asia and Oceania (and beyond) compared to other regions (Reich et al., 2010). This is probably the result of hybridization with early *H. sapiens* populations that spread eastward. It may suggest that, by the end of the MP, the range of Denisovans had expanded enough to include much of mainland Asia. The same analyses have also revealed the close genetic affinity between Denisovans and other human populations of the MP. Some paleogenetic data suggest they were closer to the Neanderthals (nDNA; Prüfer et al., 2014; Meyer et al., 2016), whereas in other analyses they were equally distant from both *H. neanderthalensis* and *H. sapiens* (mtDNA and Y chromosome, Meyer et al., 2014; Post et al., 2017; Petr et al., 2020).

Furthermore, from a phenotypic perspective, some Asian fossils dated to around 200 ka - such as those from Maba (characterized by a Neanderthal-like double-arched supraorbital torus and endocranial morphology, Wu and Bruner, 2016), Xujiayao, and Xuchang (which show traces of a suprainiac fossa, also typical among Neanderthals, Li et al., 2017) - exhibit highly derived features and may represent the as-yet-unknown morphology of the Denisovans, possibly indicating repeated interbreeding with Neanderthals. However, currently, their unequivocal taxonomic attribution is not possible (in fact, no Linnean denomination for the Denisovans has been proposed so far), due to the lack of a clear association between morphology and genetic identity in diagnostic findings.

3.3. EUROPE (WESTERN EURASIA)

Following the normal geomagnetic polarity of Jaramillo (between 1,000 and 900 ka), when the periodicity of glacial cycles extends to approximately 100 thousand years, and more specifically at the beginning of the MP, after 780 ka (Matuyama-Brunhes inversion), a faunal turnover is observed, marking the disappearance of the so-called "Villafranchian faunas" (Manzi et al., 2011). In this changed environmental context, the lithic industries of the Lower Paleolithic of Mode 1 or Oldowan exhibit a sort of rarefaction (Muttoni et al., 2010), suggesting a significant demographic contraction of human populations, if not their complete disappearance.

Subsequently, after about 650 ka (MIS 16), the first occurrences of Mode 2 or Acheulean Lower Paleolithic assemblages is documented in Europe, found in association with human remains (Moncel et al., 2020), such as in the site of Venosa-Notarchirico (Basilicata) and Visogliano (Friuli), using the Italian peninsula as an example. These human specimens exhibit a new and more derived morphology compared to the human species documented in the late Lower Pleistocene (*i.e.*, *H. antecessor*). Therefore, both the lithic industries and the morphologies of the fossil samples indicate a clear discontinuity around the Matuyama-Brunhes boundary (Manzi, 2004; Manzi et al., 2011), showing affinities with African contexts that suggest a possible diffusion route into Europe starting from Africa and passing through the Middle East.

In the Middle East, sites with Acheulean technologies of probable African origin have been documented: before 1,350 ka (Ubeidiya, Israel) and from 750 ka onwards (Gesher Benot Ya'aqov, Israel). This observation may be related to a significant series of archaeological sites and fossil human remains distributed in the mid-low latitudes of the entire continent after 700 ka, including Isernia, Venosa, and Visogliano in Italy, Boxgrove in England, Arago in southern France, Mala Balanica in Serbia, and Mauer in Germany (Dean et al., 1998; Hublin, 2009; Mounier et al., 2009).

It is not irrelevant, from this perspective, that Mauer and the mandibles found in the Arago cave (near Tautavel, in the French Pyrenees) do not show significant affinities with those of *H. antecessor* (Gran Dolina in the Sierra de Atapuerca, Spain), while they exhibit similarities with the mandibles from Tighenif (Ternifine, in Algeria), dated to more than 700 ka (Mounier et al., 2009). This reinforces the idea that *H. heidelbergensis* appeared in Africa and then spread to Eurasia, bringing Acheulean artifacts (Profico et al., 2016). This also supports the hypothesis that this species, rather than *H. antecessor*, was the common ancestor of Neanderthals (as well as *H. sapiens* in Africa and Denisovans in Asia). Furthermore, like other European fossils of similar age (for example, the calvarium from Ceprano in central Italy; Manzi, 2016), these mandibles do not exhibit clearly derived Neanderthal traits (Mounier et al., 2011, Di Vincenzo et al., 2017).

The cave site known as Sima de los Huesos is also of great interest: it is another extraordinary example of the paleoanthropological richness of the Sierra de Atapuerca (in Northern Spain). In this cave site, the skeletons of at least 29 individuals, dated to around 430 ka (Arsuaga et al., 1997, 2014; Quam et al., 2023), are preserved. Unlike the previously mentioned findings (Mauer, Arago, Ceprano), the fossil record of Sima de los Huesos clearly shows many derived Neanderthal morphological traits. This suggests - in agreement with genetic data, particularly nuclear DNA (Meyer et al., 2016) - the existence of an evolving phylogenetic lineage in Europe that spans the second half of the MP and leads to the identity of the derived species *H. neanderthalensis*.

This type of anagenetic (univocal and gradual) evolution of European populations during the MP is referred to as the “accretion model” (Dean et al., 1998). It postulates the existence of two chrono-species in Europe, *H. heidelbergensis* and *H. neanderthalensis*, with successive stages of morphological changes transitioning from archaic (plesiomorphic) features to derived Neanderthal traits (see figure 3). According to the “accretion model” - as well as to other competing scenarios like the “organismic model” (Rosas et al., 2006) - human populations in Europe underwent phases of geographical isolation and recurrent demographic crises (bottlenecks). These phases were probably connected to the alternation of glacial and interglacial periods during the MP, particularly pronounced north of the Mediterranean.

In this perspective, the cyclical expansion of glacial layers would have repeatedly led to the fragmentation of human populations, resulting in significant demographic reductions, with differential extinctions in the Central-Northern regions and the survival of small, isolated populations in more Southern and temperate refuge areas. Therefore, during each glacial cycle, only a portion of the original variability would have been preserved, and new variants – with their related effects in terms of natural selection (adaptations to cold) and genetic drift (neutral traits) – could have become fixed in a few generations. The available genetic data appears to support a similar scenario (Posth et al., 2017; Petr et al., 2020). These variants - with the characteristics acquired during population bottleneck phases - would then have had the opportunity to spread when populations expanded towards the north and came into contact again during subsequent interglacial phases. The succession of these contractions and expansions, along with their respective effects, would have resulted in a gradual accumulation and progressive fixation of derived Neanderthal features.

However, a debated point concerns the fossil record of the central phase of the MP (between MIS 12 and MIS 8). There are finds - such as Swanscombe in England, Reilingen and Steinheim in Germany, Aroeira in Portugal, and the sample from Sima de los Huesos in Spain - that exhibit apomorphic skeletal and craniodental features that bring them closer to Neanderthal morphology (Dean et al., 1998; Hublin, 2009). Within the same chronological interval, there are other human remains - such as Ceprano in Italy, Bilzingsleben in Germany, Vértesszöllös in Hungary, Petralona in Greece - which, however, do not show a significant and generalized presence of Neanderthal-derived traits, and in some morphological regions, they are decidedly more plesiomorphic (Mounier et al., 2009, 2011). Therefore, there is considerable variability in the European MP, with fossil specimens (even nearly contemporaneous ones) morphologically oriented towards Neanderthal characteristics, while others are less so or not at all similarly derived (Fig. 3).

To further complicate the story, some authors have pointed out the possibility that fossil specimens, such as

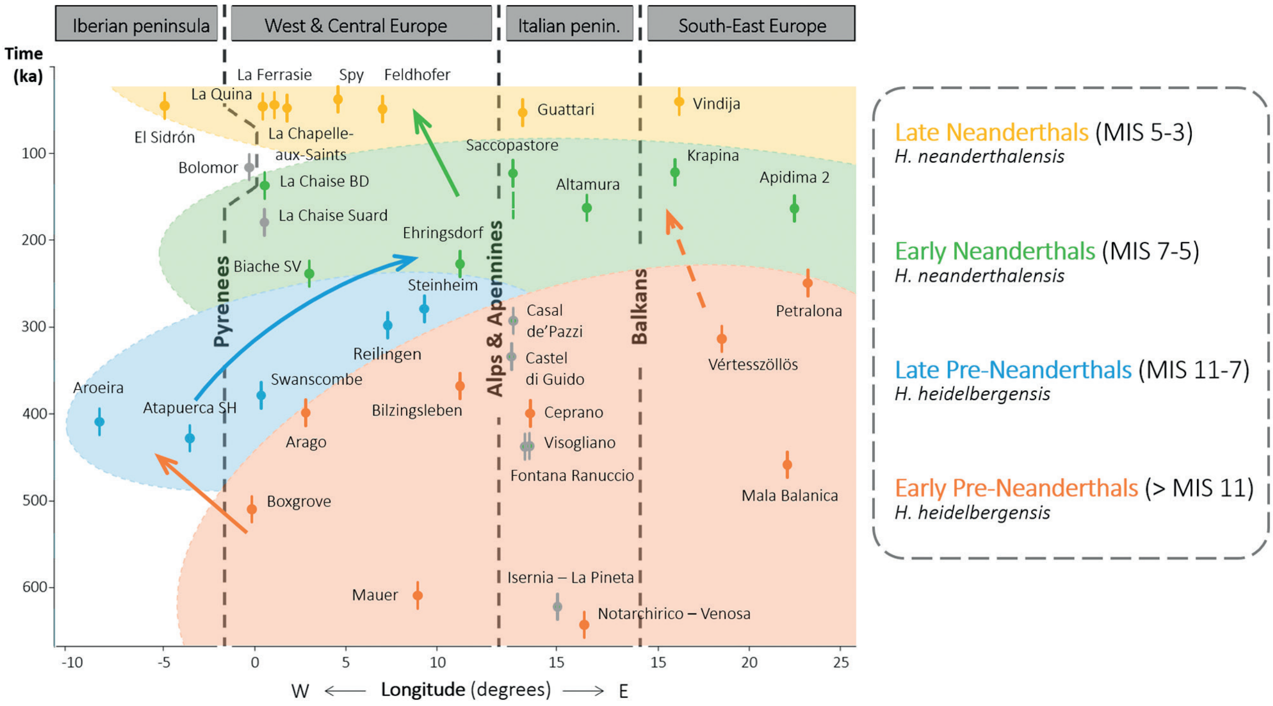

Fig. 3 - A phylogeographic scenario for human evolution in Europe during the MP. Overall, a progression of increasing Neanderthal affinity is observed not only over time, but also from West to East (blue arrow). This scenario is partially consistent with the “accretion model” of Neanderthal evolution (Dean et al., 1998), whose terminology is indicated in the right column of this graph. Actually, compared to this model, biogeographic and latitudinal aspects are also taken into consideration. The colors indicate the alleged taxonomic status of the various samples (as in the legend on the right), whereas specimens with uncertain or controversial attribution are represented in gray.

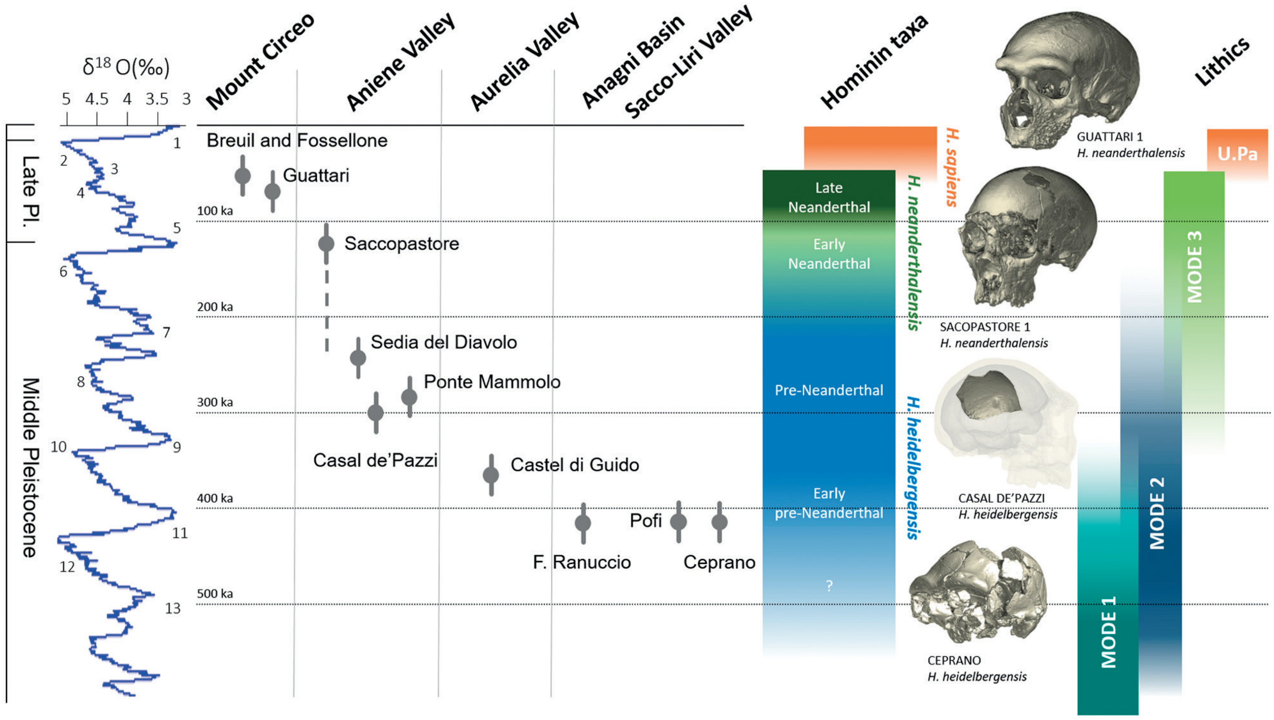

Fig. 4 - Latium (central Italy, Tyrrhenian side) provides representative human fossil specimens that are consistent with the pattern of human evolution in Europe during the Middle and Late Pleistocene. These include, among other samples, the Ceprano calvarium in the Sacco-Liri Valley (Frosinone), the Casal de' Pazzi parietal bone and the Saccopastore crania in the Aniene Valley (Rome), as well as the Würmian Neanderthals from Grotta Guattari (Mount Circeo promontory). The diagram represents (with gray bars) the chronological distribution of sites that have yielded fossil hominins, within the context of climatic fluctuations (marine isotope stages or MIS; on the left); the terminology adopted by proponents of the "accretion model" and the main techno-typological cultures of the archaeological record (on the right) are also reported.

those from Sima de los Huesos, can already be attributed to *H. neanderthalensis* (Hublin, 2009), effectively excluding *H. heidelbergensis* from the role of the LCA. However, this interpretation is partially contradicted on a genetic basis when the signal from mtDNA - similar to that of Denisovans and likely shared within the variability of the LCA - is combined with the signal from nDNA, which is closer to the later identity of *H. neanderthalensis*. The topologies of phylogenetic trees reconstructed based on the available genetic data (Meyer et al., 2014, 2016) tend to exclude the possibility that the sample from Sima de los Huesos and the Neanderthals form together the same taxonomic group, given the inclusion of the Denisovans (when we consider the mtDNA) or because the low resolution (in the case of nDNA).

The geographical distribution of fossil samples in Europe and their evolving morphologies suggest that Neanderthal traits appeared early in the Western and Atlantic regions of the continent (Roksandic et al., 2018) and only later spread eastward into Central Europe, peninsular Italy, and the Balkans, eventually reaching the Middle East, where Neanderthals may have replaced more ancestral human populations that were already present there (Manzi, 2016). We suggest therefore a "phylogeographic" evolutionary scenario (Fig. 3) that takes into account not only the chronology (as in the "accretion model") but also the geographical and latitudinal distribution of human specimens from the MP in Europe (Anagnostou et al., 2022; Profico et al., 2023).

From this perspective, the parietal bone of Casal de' Pazzi (CdP-H1), with its plesiomorphic morphology (Manzi et al., 1990) and its presumed chronology dating back over 250 ka, fits well into this scenario of progressive change toward more derived humans that after MIS8 are eventually attributed to *H. neanderthalensis* (Fig. 5; see also figure 4).

CdP-H1 was discovered in May 1983 (Passarello et al., 1985), deeply embedded in a stratigraphic horizon belonging to the lowest layer of the homonymous fluvial deposit, directly in contact with the rocky riverbed (Anzidei and Ruffo, 1985; Bietti, 1985). Despite its small dimensions, this fragment of the right parietal bone exhibits features such as relatively high thickness (10.15-6.45 mm), the degree and profile of its paracoronal curvature, absence of the parietal foramen, and the type of endocranial vascularization, which distinguish it (at least partially) from the corresponding cranial region of *H. erectus (sensu lato)*, Neanderthals, and anatomically modern humans. At the same time, it shows morphological affinities with other MP specimens. Therefore, as early as in 1990, Manzi, Salvadei, and Passarello concluded that the archaic human parietal from Casal de' Pazzi should be assigned to what was then called "the 'archaic *H. sapiens*' group", falling within the range of pre-Neanderthal

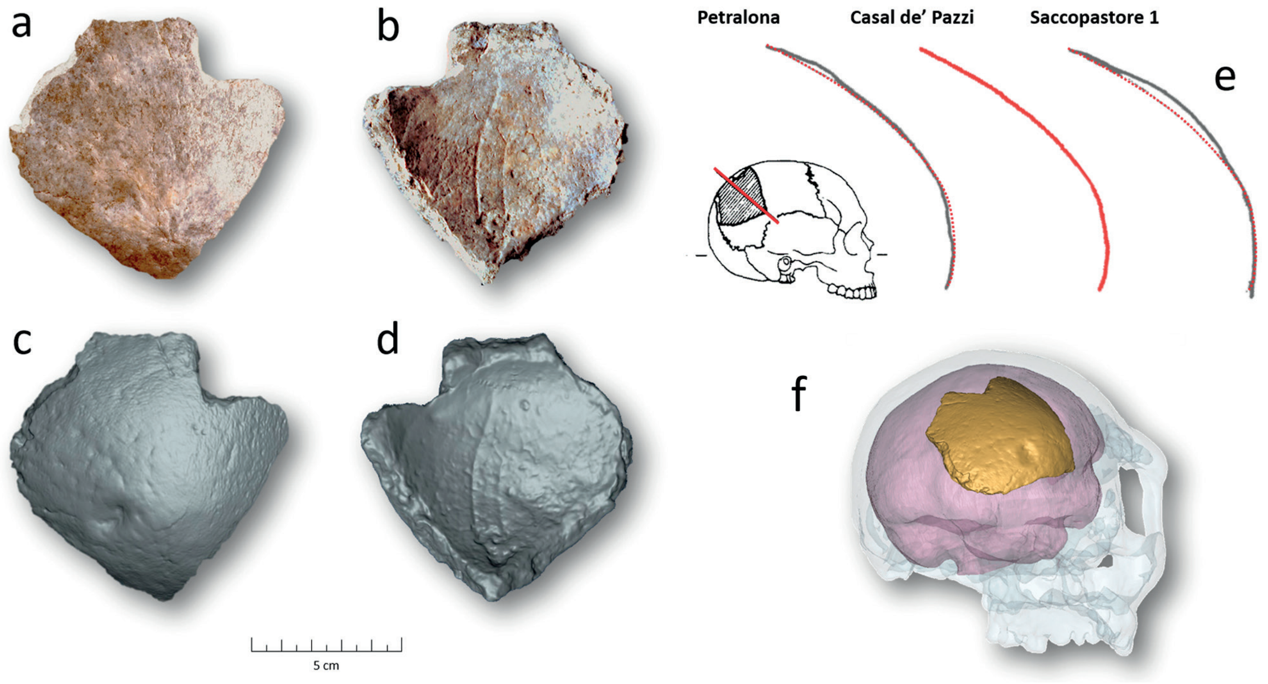

Fig. 5 - The right parietal bone CdP-H1 was found in 1983 during excavations at Casal de' Pazzi in the Aniene Valley, Rome (Italy). On the left, the external (a) and endocranial (b) surfaces of CdP-H1 are shown, along with corresponding computed tomography images (c-d, same scale): the fragment is oriented with the sagittal suture facing upward, while a remnant of the lambdoid suture occurs posteriorly; on the external surface, a circular depression is visible, likely due to trauma, while internally, there are the branches of meningeal vascularization. On the right (e), the paracoronal profile of CdP-H1 (in red) is superimposed on those of two comparative specimens (Manzi et al., 1990): it can be observed that the profile of CdP-H1 matches that of Petralona (*H. heidelbergensis*), while it differs from Saccopastore 1 (*H. neanderthalensis*), lacking the typical "en bombe" morphology of Neanderthals. The anatomical position of CdP-H1 is also shown (f), superimposed on the outline of the penecontemporaneous cranium from Petralona (Greece).

variability in Europe. According to the scenario of human evolution discussed in this review, it may thus be attributed to *H. heidelbergensis.*

In conclusion, the possibility that *H. heidelbergensis* (when the Mauer mandible is included in the hypodigm; Mounier et al., 2009, 2011) might represent the LCA - a highly variable taxon composed of geographically semi-isolated populations (paleodemes or subspecies; Manzi, 2016) whose divergence increased over time - is consistent with ecological models proposed to explain the evolution of Neanderthals in Europe. The presence of evolving paleodemes within such a polymorphic species is a condition that we have also observed in Africa and continental Asia during the MP, with modalities that are similar (at least in part) to what we have eventually described for Europe.

ACKNOWLEDGEMENTS - Given the context of this volume dedicated to the Middle Pleistocene site of Casal de' Pazzi (Roma, Italy), in this paper we will give more emphasis to the European fossil record. It must be added that, still today, the picture we have for Europe (despite the different points of view expressed by some researchers) appears clearer and more explainable than those we have for both Africa and Asia.

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REFERENCES

Anagnostou P., Montinaro F., Sazzini M., Di Vincenzo F., Destro Bisol G., 2022. From the Alps to the Mediterranean and beyond: genetics, environment, culture and the" impossible beauty" of Italy. Journal of Anthropological Sciences 100, 267-294.

Anton S.C., 2004. The face of Olduvai Hominid 12. Journal of Human Evolution 46, 335-45.

Anzidei A.P., Ruffo M., 1985. The Pleistocene deposit of Rebibbia-Casal de' Pazzi, Rome, Italy. In: Malone C., Stoddart S., (Eds.), Papers in Italian Archaeology IV: part I - The Human Landscape, BAR Internat. Ser., 243, 68-85.

Arambourg C., 1954. L'hominien fossile de Ternifine, Algerie. Comptes Rendus de l'Académie des Sciences de Paris 239, 893-895.

Arambourg C., 1955. A recent discovery in human paleontology:

Atlanthropus of Ternifine, Algeria. American Journal of Physical Anthropology 13, 191-201.

Arsuaga J.L., Martínez I., Arnold L.J., Aranburu A., Gracia-Téllez A., Sharp W.D., Quam R.M., Falguéres C., Pantoja-Pérez A., Bischoff J., 2014. Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. Science 344, 1358-1363.

Arsuaga J.L., Martínez I., Gracia A., Carretero J.M., Lorenzo C., Garcıa N., Ortega A.I., 1997. Sima de los huesos., Sierra de Atapuerca., Spain. The site. Journal of Human Evolution, 33, 109-127.

Arsuaga J.L., Martínez I., Lorenzo C., Gracia A., Munoz A., Alonso O., Gallego J., 1999. The human cranial remains from Gran Dolina Lower Pleistocene site, Sierra de Atapuerca., Spain. Journal of Human Evolution 37, 431-57.

Asfaw B., Gilbert W.H., Beyene Y., Hart W.K., Renne P.R., Woldegabriel G., Vrba E.S, White T.D., 2002. Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia. Nature 416, 317-20.

Berckhemer F., 1936. Der Urmenschenschädel aus den zwischeneiszeitlichen Fluß-Schottern von Steinheim an der Murr. Forschungen und Fortschritte 12, 349-350.

Berger L.R. , Hawks J., de Ruiter D.J., Churchill S.E., Schmid P., Delezene L.K., Kivell T.L., Garvin H.M., Williams S.A., DeSilva J.M., Skinner M.M., Musiba C.M., Cameron N., Holliday T.W, Harcourt-Smith W., Ackermann R.R., Bastir M., Bogin B., Bolter D., Brophy J., Cofran Z.D., Congdon K.A., Deane A.S., Dembo M., Drapeau M., Elliott M.C., Fuerriegel E.M., Garcia-Martinez D., Green D.J., Gurtov A., Irish J.D., Kruger A., Laird M.F., Marchi D., Meyer M.R., Nalla S., Negash E.W., Orr C.M., Radovcic D., Schroeder L., Scott J.E., Throckmorton Z., Tocheri M.W., VanSickle C., Walker C.S., Pianpia Wei P., Zipfel B., 2015. *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. eLife 4, e09560.

Bergström A., Stringer C., Hajdinjak M., Scerri E.M.L., Skoglund P., 2021. Origins of modern human ancestry. Nature 590, 229-237.

Bietti A., 1985. A late Rissian Deposit in Rome: Rebibbia-Casal de' Pazzi. In: Delson E. (Ed.), Ancestors: The Hard Evidence. A.R. Liss., New York, 277-282.

Bräuer G., 2012. Middle Pleistocene diversity in Africa and the origin of modern humans. In: Hublin J.-J., McPherron S.P. (Eds.), Modern Origins: a North African perspective. Springer, 221-240.

Brown P., Sutikna T., Morwood M.J., Soejono R.P., Wayhu Saptomo E., Awe Due R., 2004. A new small-bodied hominin from the Late Pleistocene of Flores., Indonesia. Nature 431, 1055-1061.

Bruner E., Manzi G., Arsuaga J.L., 2003. Encephalisation and allometric trajectories in the genus *Homo*. Evidence from the Neandertal and modern lineages. Proceedings of the National Academy of Sciences USA 100, 15335-15340.

Bruner E., Pearson O., 2013. Neurocranial evolution in modern humans: the case of Jebel Irhoud 1. Anthropological Science 121, 31-41.

Buck L.T., Stringer C.B., 2014. *Homo heidelbergensis*. Current Biology 24, 214-215.

Carbonell E., Bermúdez de Castro J.M., Arsuaga J.L., Díez J.C., Rosas A., Cuenca-Bescós G.. Sala R. Mosquera M., Rodríguez X-P., 1995. Lower Pleistocene hominids and artifacts from Atapuerca-TD6, Spain. Science 269, 826-830.

Carbonell E., Bermúdez de Castro J.M., Parés J.M., et al., 2008. The first hominin of Europe. Nature 452, 465-469.

Caspari R., Wolpoff M.H., 1996. Weidenreich, Coon, and multiregional evolution. Human evolution 11, 261-268.

Chan E.K.F., Timmermann A., Baldi B.F., Moore A.E., Lyons R.J., Lee S-S., Kalsbeek A.M.F., Petersen D.C., Rautenbach H., Förtsch H.E.A., Bornman M.S.R., Hayes V.M., 2019. Human origins in a southern African palaeo-wetland and first migrations. Nature 575, 185-189.

Chen F., Welker F., Shen C-C., Bailey S.E., Bergmann I., Davis S., Xia H., Wang H., Fischer R., Freidline S.E., Yu T-L., Skinner M.M., Stelzer S., Dong G., Fu Q., Dong G., Wang J., Zhang D., Hublin J-J., 2019. A late Middle Pleistocene Denisovan mandible from the Tibetan Plateau. Nature 569, 409-412.

Clark P.U., Archer D., Pollard D., Blum J.D., Rial J.A., Brovkin V., Mix A.C., Pisias N.G., Roy M., 2006. The Middle Pleistocene transition: characteristics, mechanisms, and implication for long-term changes in atmospheric pCO_2. Quaternary Science Reviews 25, 3150-3184.

Cohen K.M., Harper D.A.T., Gibbard P.L., 2020. ICS International Chronostratigraphic Chart 2020/03: International Commission on Stratigraphy, IUGS. Updated at: www. stratigraphy.org.

Day M.H., Stringer C.B., 1991. Les restes craniens d'Omo-Kibish et leur classification a l'interieur du genre *Homo*. Anthropologie 95, 573-594.

Dean D., Hublin J-J., Holloway R., Ziegler R., 1998. On the phylogenetic position of the pre-Neandertal specimen from Reilingen, Germany. Journal of Human Evolution 34, 485-508.

Delson E., Stringer C.B., 2022. The naming of *Homo bodoensis* by Roksandic and colleagues does not resolve issues surrounding Middle Pleistocene human evolution. Evolutionary Anthropology 31, 233-236.

Demeter F., Zanolli C., Westaway K.E., Joannes-Boyau R., Duringer P., Morley M.W., Welker F., Rüther P.L., Skinner M.M., McColl H., 2022. A Middle Pleistocene Denisovan molar from the Annamite chain of northern Laos. Nature communications 13, 2557.

Detroit F., Mijares A.S., Corny J., Daver G., Zanolli C., Dizon E., Robles E., Grün R., Piper P.J., 2019. A new species of *Homo* from the Late Pleistocene of the Philippines. Nature 568, 181-86.

Di Vincenzo F., Profico A., Bernardini F., Cerroni V., Dreossi D., Schlager S., Zaio P., Benazzi S., Biddittu I., Rubini M., Tuniz C., Manzi G., 2017. Digital reconstruction of the Ceprano calvarium, Italy, and implications for its interpretation. Scientific Reports 7, 13974.

Drennan M.R., 1955. The special features and status of the Saldanha skull. American Journal of Physical Anthropology 13, 625-34.

Dreyer T., 1935. A human skull from Florisbad, Orange Free State., with a note on the endocranial cast, by Ariens Kappers C.V. Proceedings of the Academy of Science, Amsterdam 38, 119-128.

Dubois E., 1893. Palaeontologische onderzoekingen op Java. Versalg van het Mijnwezen. Batavia Third Quarter, 10-14.

Etler DA., 1996. The fossil evidence for human evolution in Asia. Annual Review of Anthropology 25, 275-301.

Foley R.A., Lahr M.M., 1997. Mode 3 technologies and the evolution of modern humans. Cambridge Archaeological Journal 7, 3-36.

Groves C.P., Mazak V., 1975. An approach to the taxonomy of the Hominidae: gracile Villafranchian hominids of Africa. Casopsis pro mineralogii a geologii 20, 225-247.

Grün R., Pike A., McDermott F., Eggins S., Mortimer G., Aubert M., Stringer C., 2020. Dating the skull from Broken Hill, Zambia, and its position in human evolution. Nature 580, 372-375.

Gunz P., Neubauer S., Maureille B., Hublin J-J., 2010. Brain development after birth differs between Neanderthals and modern humans. Current Biology 20, 921-922.

Harvati K., Reyes-Centeno H., 2022. Evolution of *Homo* in the Middle and Late Pleistocene. Journal of Human Evolution 173, 103279.

Head M.J., Gibbard P.L. (Eds.), 2005. Early-Middle Pleistocene Transition: The land-Ocean Evidence. Geological Society, London, Special Publications 247, 1-18.

Hu W., Hao Z., Du P., Di Vincenzo F., Manzi G., Cui J., Fu YX., Pan YH., Li H., 2023. Genomic inference of a severe human bottleneck during the Early to Middle Pleistocene transition. Science (in press).

Hublin J-J., 2009. The origin of Neandertals. Proceedings of the National Academy of Sciences USA 106, 16022-16027.

Hublin, J-J., Ben-Ncer A., Bailey S.E., Freidline S.E., Neubauer S., Skinner M.M., Bergmann I., Le Cabec A., Benazzi S., Harvati K., 2017. New fossils from Jebel Irhoud., Morocco and the pan-African origin of *Homo sapiens*. Nature 546, 289-292.

Ji Q., Wu W., Ji Y., Li Q., Ni X., 2021. Late Middle Pleistocene Harbin cranium represents a new *Homo* species. The Innovation 2, 100132.

Krause J., Fu Q., Good JM., Viola B., Shunkov M.V., Derevianko A.P., Pääbo S., 2010. The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. Nature, 464, 894-897.

Lahr M.M., Foley R.A., 1998. Towards a theory of modern human origins: geography, demography and diversity on recent human evolution. Annual Review of Anthropology 27, 137-176.

Li Z.Y., Wu X.J., Zhou L.P., Liu W., Gao X., Nian X.M., Trinkaus E., 2017. Late Pleistocene archaic human crania from Xuchang, China. Science, 355, 969-972.

Macchiarelli R., Bondioli L., Chech M., Coppa A., Fiore I., Russom R., Vecchi F., Libsekal Y., Rook L., 2004. The late early Pleistocene human remains from Buia, Danakil Depression, Eritrea. Rivista Italiana di Paleontologia e Stratigrafia 110, 133-44.

Manzi G., 2003. "Epigenetic" cranial traits, Neandertals and the origin of *Homo sapiens*. Rivista di Antropologia 81, 57-67.

Manzi G., 2004. Human evolution at the Matuyama-Brunhes boundary. Evolutionary Anthropology 13, 11-24.

Manzi G., 2016. Humans of the Middle Pleistocene: the controversial calvarium from Ceprano, Italy, and its significance for the origin and variability of *Homo heidelbergensis*. Quaternary International 411, 254-261.

Manzi G., Salvadei L., Passarello P., 1990. The Casal de' Pazzi archaic parietal: comparative analysis of new fossil evidence from the late Middle Pleistocene of Rome. Journal of Human Evolution 19, 751-759.

Manzi G., Magri D., Palombo M.R., 2011. Early-Middle Pleistocene environmental changes and human evolution in the Italian peninsula. Quaternary Science Reviews 30, 1420-1438.

Massilani D., Skov L., Hajdinjak M., Gunchinsuren B., Tseveendorj D., Yi S., Lee J., Nagel S., Nickel B., Deviése T., 2020. Denisovan ancestry and population history of early East Asians. Science 370, 579-583.

McBrearty S., Brooks A.S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. Journal of Human Evolution 39, 453-563.

Melchionna M., Profico A., Castiglione S., Sansalone G., Serio C., Mondanaro A., Di Febbraro M., Rook L., Pandolfi L., Di Vincenzo F., Manzi G., Raia P., 2020. From smart apes to human brain boxes. A uniquely derived brain shape in late hominins clade. Frontiers in Earth Science 8, 273.

Meneganzin A., Pievani T., Manzi G., 2022. Pan-Africanism vs. single-origin of *Homo sapiens*: Putting the debate in the light of evolutionary biology. Evolutionary Anthropology 31, 199-212.

Meyer M., Arsuaga J-L., De Filippo C., Nagel S., Aximu-Petri A., Nickel B., Martínez I., Gracia A., Bermúdez de Castro J.M., Carbonell E., 2016. Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. Nature 531, 504-507.

Meyer M., Fu Q., Aximu-Petri A., Glocke I., Nickel B., Arsuaga J-L., Martínez I., Gracia A., Bermúdez de Castro J.M., Carbonell E., 2014. A mitochondrial genome sequence of a hominin from Sima de los Huesos. Nature 505, 403-406.

Moncel M.H., Santagata C., Pereira A., Nomade S., Voinchet P., Bahain J.J., Daujeard C., Curci A., Lemorini C., Hardy B., 2020. The origin of early Acheulean expansion in Europe 700 ka ago: new findings at Notarchirico, Italy. Scientific Reports 10, 13802.

Mounier A., Condemi S., Manzi G., 2011. The stem species of our species: a place for the archaic human cranium from Ceprano, Italy. PLoS ONE 6, e18821.

MounierA and Caparros M., 2015. The phylogenetic status of *Homo heidelbergensis* - a cladistics study of Middle Pleistocene hominins. BMSAP 27, 110-134.

Mounier A., Mirazon Lahr M., 2016. Virtual Ancestor Reconstruction: revealing the ancestor of modern humans and Neandertals. Journal of Human Evolution 91, 57-72.

Mounier A., Mirazon Lahr M., 2019. Deciphering African late middle Pleistocene hominin diversity and the origin of our species. Nature Communications 10, 3406.

Mounier A., Marchal F., Condemi S., 2009. Is *Homo heidelbergensis* a distinct species? New insight on the Mauer mandible. Journal of Human Evolution 56, 219-246.

Muttoni G., Scardia G., Kent D.V., Morsiani E., Tremolada

F., Cremaschi M., Peretto C., 2010. First dated human occupation of Italy at ~0.85 Ma during the late Early Pleistocene climate transition. Earth and Planetary Science Letters 307, 241-252.

Ni X., Ji Q., Wu W., Shao Q., Ji Y., Zhang C., Liang L., Ge J., Guo Z., Li J., 2021. Massive cranium from Harbin in northeastern China establishes a new Middle Pleistocene human lineage. The Innovation 2, 100130.

Passarello P., Salvadei L., Manzi G., 1985. II parietale umano del deposito pleistocenico di Casal de' Pazzi, Roma. Rivista di Antropologia 63, 287-298.

Petr M., Hajdinjak M., Fu Q., Essel E., Rougier H., Crevecoeur I., Semal P., Golovanova L.V., Doronichev V.B., Lalueza-Fox C., 2020. The evolutionary history of Neanderthal and Denisovan Y chromosomes. Science 369, 1653-1656.

Posth C., Wiaing C., Kitagawa K., Pagani L., van Holstein L., Racimo F., Wehrberger K., Conard N.J., Kind CJ., Bocherens H., 2017. Deeply divergent archaic mitochondrial genome provides lower time boundary for African gene flow into Neanderthals. Nature communications 8, 16046.

Potts R., Behrensmeyer A.K., Deino A.L., Ditchfield P., Clark J., 2004. Small Mid-Pleistocene Hominin Associated with East African Acheulean Technology. Science 305, 75-78.

Profico A., Buzi C., Di Vincenzo F., Boggioni M., Borsato A., Boschian G., Marchi D., Micheli M., Cecchi J.M., Samadelli M., 2023. Virtual excavation and analysis of the early Neanderthal cranium from Altamura, Italy. Communications Biology 6, 316.

Profico A., Di Vincenzo F., Gagliardi L., Piperno M., Manzi G., 2016. Filling the gap. Human cranial remains from Gombore II., Melka Kunture., Ethiopia; ca. 850 ka and the origin of *Homo heidelbergensis*. Journal of Anthropological Sciences 94, 41-63.

Prüfer K., Racimo F., Patterson N., Jay F., Sankararaman S., Sawyer S., Heinze A., Renaud G., Sudmant P.H., De Filippo C., 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505, 43-49.

Quam R., Martínez I., Rak Y., Hylander B., Pantoja A., Lorenzo C., Arsuaga J-L., 2023. The Neandertal nature of the Atapuerca Sima de los Huesos mandibles. The Anatomical Record, 1-51. doi: 10.1002/ar.25190.

Reich D., Green R.E., Kircher M., Krause J., Patterson N., Durand E.Y., Viola B., Briggs A.W., Stenzel U., Johnson P.L.F., 2010. Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature 468, 1053-1060.

Reich D., Patterson N., Kircher M., Delfin F., Nandineni M.R., Pugach I., Ko A.M-S., Ko Y-C., Jinam TA., Phipps M.E., 2011. Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. The American Journal of Human Genetics 89, 516-528.

Rightmire P.G., 1996. The human cranium from Bodo, Ethiopia: Evidence for speciation in the Middle Pleistocene? Journal of Human Evolution 31, 21-39.

Rightmire G.P., 1998. Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis*. Evolutionary Anthropology 6, 218-227.

Rizal Y., Westaway K.E., Zaim Y., van den Bergh G.D., Bettis Iii E.A., Morwood M.J., Huffman O.F., Grün R., Joannes-Boyau R., Bailey R.M., 2020. Last appearance of *Homo erectus* at Ngandong, Java, 117,000-108,000 years ago. Nature 577, 381-385.

Roksandic M., Radović P., Lindal J., 2018. Revising the hypodigm of *Homo heidelbergensis*: A view from the Eastern Mediterranean. Quaternary International 466, 66-81.

Roksandic M., Radovic P., Wu X., Bae C.J., 2021. Resolving the "muddle in the middle": The case for *Homo bodoensis* sp. nov. Evolutionary Anthropology 31, 20-29.

Rosas A., Bastir M., Martinez-Maza C., Garcia-Tabernero A., Lalueza-Fox C., 2006. Inquiries into Neanderthal craniofacial development and evolution: "accretion" versus "organismic" models. In Hublin J-J., Harvati K., Harrison T., (Eds.), Neanderthals Revisited: New Approaches and Perspectives. Springer, 37-69.

Scerri E.M.L., Thomas M.G., Manica A., Gunz P., Stock J.T., Stringer C., Grove M., Groucutt H.S., Timmermann A., Rightmire G.P., 2018. Did our species evolve in subdivided populations across Africa, and why does it matter? Trends in Ecology and Evolution 33, 582-594.

Schoetensack O., 1908. Der unterkiefer des *Homo heidelbergensis* aus den Sanden von Mauer bei Heidelberg. Ein Beitrag zur Paläontologie des Menschen. Zeitschrift für induktive Abstammungs- und Vererbungslehre 1, 408-410.

Slon V., Mafessoni F., Vernot B., De Filippo C., Grote S., Viola B., Hajdinjak M., Peyrégne S., Nagel S., Brown S., 2018. The genome of the offspring of a Neanderthal mother and a Denisovan father. Nature 561, 113-116.

Stringer C.B., 1983. Some further notes on the morphology and dating of the Petralona hominid. Journal of Human Evolution 12, 731-42.

Stringer C.B., 2018. The status of *Homo heidelbergensis*, Schoetensack 1908. Evolutionary Anthropology 21, 101-107.

Stringer C.B., 2022. The development of ideas about a recent African origin for *Homo sapiens*. Journal of Anthropological Sciences JASS 100, 5-18.

Stringer C.B., Andrews P., 1988. Genetic and fossil evidence for the origin of modern humans. Science 239, 1263-1268.

Vernot B., Tucci S., Kelso J., Schraiber J.G., Wolf A.B., Gittelman R.M., Dannemann M., Grote S., McCoy R.C., Norton H., 2016. Excavating Neandertal and Denisovan DNA from the genomes of Melanesian individuals. Science 352, 235-239.

Yamei H., Potts R., Baoyin Y., Zhengtang G., Deino A., Wei W., Clark J., Guangmao X., Weiwen H., 2000. Mid-Pleistocene Acheulean-like stone technology of the Bose basin, South China. Science 287, 1622-1626.

Vidal C.M., Lane C.S., Asrat A., Barfod D.N., Mark D.F., Tomlinson E.L., Oppenheimer C., 2022. Age of the oldest known *Homo sapiens* from eastern Africa. Nature 601, 579-583.

Weidenreich F., 1947. Facts and speculations concerning the origin of *Homo sapiens*. American Anthropologist 49, 187-203.

Woodward A.S., 1921. A new cave man from Rhodesia. South Africa. Nature 108, 371-372.

Wu X., 1981. A well-preserved cranium of an archaic type of early *Homo sapiens* from Dali, China. Scientia Sinica 24, 530-539.

Wu X., Bruner E., 2016. The endocranial anatomy of Maba 1. American Journal of Physical Anthropology 160, 633-643.

Zatrev J., 2014. The co-evolution of human intersubjectivity, morality, and language. In: Dor D., Knight C., Lewis J., (Eds). The Social Origins of Language. Oxford University Press, 249-266.