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THE RISE AND SPREAD
OF *HOMO SAPIENS*

GERRIT HEINRICH KROON
(1868-1945)

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DOOR

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INTRODUCTION

*F*or around 40,000 years, our planet has been populated by a single species of hominin that had unprecedented reproductive success and colonized all emerging lands: *Homo sapiens*. Although displaying a great deal of diversity from one continent to another in relation to different kinds of climates and environments, *Homo sapiens* are – from a genetic point of view – remarkably homogeneous. This results from a recent common origin for all living humans and contrasts with the situation that prevailed for the previous seven million years (Figure 1).
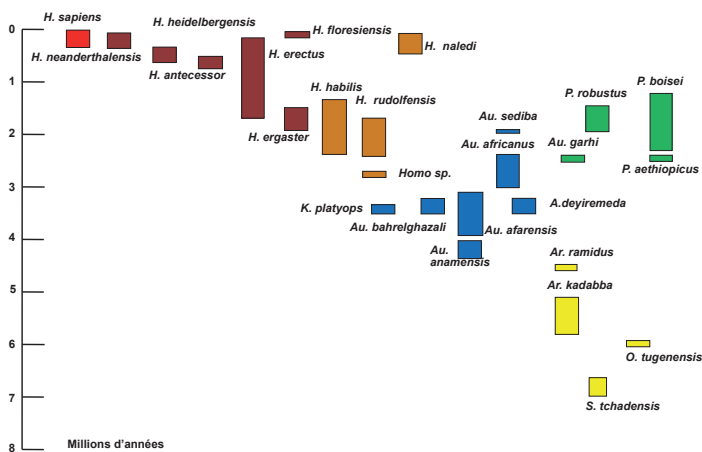

Figure 1. Chronological extension of the various paleontological species of hominins that have been identified in the course of the last 7 million years. Adapted from Wood, 2010.

For the majority of time since the Miocene epoch to almost the end of the Pleistocene, several groups of hominins coexisted on Earth, sometimes even in the same continental regions (Wood, 2010). These groups are generally recognized as paleontological species and are separated from our own species. Following the suggestions of Theodore Dobzhansky (1900-1975), the most popular and successful definition of species was provided by the biologist Ernst Mayr (1904-2005). His concept of biological species is based on the notion that "species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr, 1942). However, this definition that emphasizes the role of reproductive isolation is not the only one. More than twenty-five others which put forward ecological, morphological, or genetic criteria have also been proposed, and many of them are not less biological than that of the "biological species" (De Queiroz, 2007). Critically, at present, the very notion of biological species is more blurred than previously believed.

Even if the notion of interbreeding communities seems straightforward, the reality is more complicated. Reproductive isolation generally does not appear as a rapid event. It is often the result of a long process that can take several million years for midsized mammals (Holliday, 2003). Geographic and genetic isolation results in morphological and ecological divergences and the accumulation of genetic differences that make potential reproduction between representatives of two different developing species more and more difficult. This results in the gradual reduction of their reproductive compatibility, eventually leading to compete reproductive isolation. The rapid development of high throughput gene sequencing in recent years has shown that many species of mammals that are closely related, though widely recognized as separate, have retained some capacity for interbreeding and have exchanged some genetic material in the course of their recent evolution (Asensio et al., 2017; Hassanin, 2015; Palkopoulou et al.,

2018). Furthermore, the biological concept of species cannot be easily applied to the fossil record as interbreeding among extinct organisms is impossible to assess without access to their genomes, and genomes are currently accessible only for the relatively recent periods of the past. Another difficulty results from the fact that extinct species can cover a long span of time and often display significant evolutionary changes during their existence. Through time, species include individuals that never coexisted and therefore could not breed. Similar to difficulties in recognizing contemporaneous genuine species, there are also serious challenges in defining the chronological limits of past species. All of these issues had to be entertained by those who attempted to define *Homo sapiens* not only as a living species but also as a paleontological species.

The term of *Homo sapiens* was first proposed by Carl Linnaeus (1707-1778) in his famous work *Systema Naturae*. At that time, there was little resistance to dividing *Homo sapiens* into various sub-species coinciding with the races that were then recognized. Other species of humans, such as *Homo troglodytes*, were also accepted by many before being rejected as imaginary forms by Johann Friedrich Blumenbach (1752-1814). Blumenbach emphasized that all extant humans belonged to a single species, *Homo sapiens* (Blumenbach, 1775). In the fossil record, the notion of *Homo sapiens* is often equated with that of "anatomically modern humans." Today's humans are characterized by a set of anatomical features, including skeletal traits, that distinguish them from archaic forms of earlier hominins. These features are quite recognizable on the skull and the mandible. Living humans display a round shaped brain case with a globular profile, under which the face is retracted. The shortened face is therefore dominated by a round and vertically placed forehead that does not display strong reliefs. The lateral sides of the skull are flattened and the rear part is rounded without backward projection. The

mandible has a unique shape with a bony chin variably project-
ing forward.

To what extent ancient humans directly related to our ancestry
exhibited the present-day variation of these features has been the
subject of many debates. Moving back in time, one quickly meets
populations that are obviously connected to living populations
but which also display significant anatomical differences. There-
fore, the concept of *Homo sapiens* is different from that of ana-
tomically modern humans, the latter representing an ill-defined
and recent sub-group of the former. Differing views regarding the
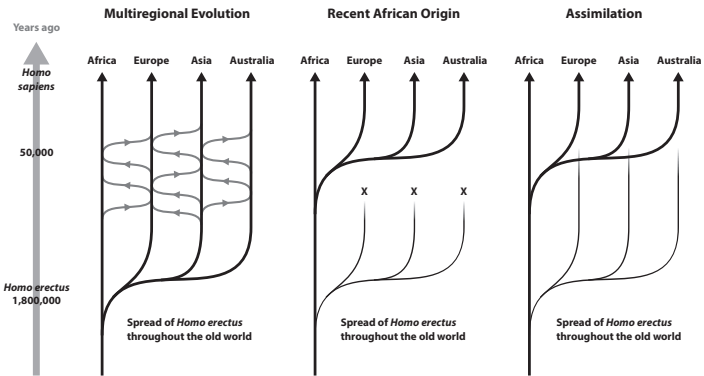process of emergence of living populations also fueled debates

*Figure 2. Schematic representation of three theoretical models of origin
for recent populations of Homo sapiens. The Multiregional model
proposed long local continuities after the spread of Homo erectus
out of Africa, with some gene flow across continents. The Recent
African Origin model posits a complete extinction of the local archaic
population at the time of the final spread of Homo sapiens over the
Old World. The Assimilation model assumes a significant level of
admixture between local hominins and Homo sapiens immigrants at
the time of the replacement.*

surrounding the definition of *Homo sapiens*. In contrast with the current notion of a rather recent common origin of all living humans, the now largely falsified concept of a more or less separated emergence of several large groups of living humans was long entertained. Polycentric (Coon, 1962; Weidenreich, 1946) and later multiregional models (Wolpoff, 1989) posited that these populations were rooted in distinct groups of archaic hominins that lived in different parts of the Old World (Figure 2).

THE MIDDLE PLEISTOCENE DIVERSIFICATION

The development of *Homo sapiens* took place in a period of time that witnessed the evolution of other hominin groups (Figure 3). While the oldest forms of *Homo sapiens* are only known in Africa,
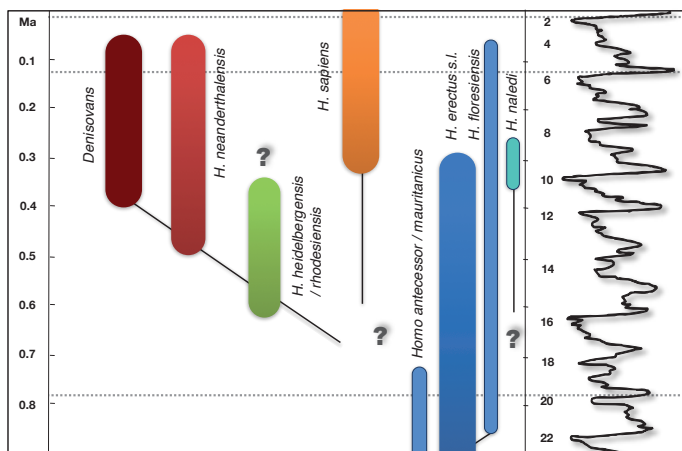

Figure 3. On the left, diversification of hominin groups from the Late Early Pleistocene to present day. On the right, the main glacial stages are indicated by numbers along the paleoclimatic curve established from oceanic oxygen isotopes.

widely recognized as the cradle of our species, Eurasia hosted other species of hominins that were eventually replaced or partially absorbed by *Homo sapiens* in the late Pleistocene. The Neandertals are the most studied of these groups and are best represented in the fossil record. Their remains were first found in western Europe in the second half of the 19th century. Later these populations were documented in southwest Asia and throughout the middle latitudes of Eurasia, as far east as the Altai mountains. In Asia, a closely related group of hominins known as "Denisovans" was identified in 2010 in the Altai mountains where they occasionally overlapped and hybridized with Neandertals (Krause et al., 2010; Slon et al., 2018). Denisovans are presently only identified by their genome. Their morphology remains mysterious due to the fragmentary nature of the fossils that have yielded their DNA. However, it is likely that their populations or populations related to them were present in a large portion of continental Asia where more complete specimens have been found. Unfortunately, to date, these specimens have not yielded any ancient DNA.

Ancient forms of *Homo sapiens*, Neandertals, and Denisovans can be seen as distinct lineages. The first two of these at least display very distinctive anatomical cranial mandibular features (Figure 4). However, one must also highlight that they display common features. Specifically, *Homo sapiens*, Neandertals, and likely Denisovans, displayed larger brains than previous hominins, a trend that might be connected to increasing behavioral complexity in all of these groups. Their diverging evolution was driven by geographical isolation as well as adaptation to different environments. Environmental changes that affected the climatic cycles throughout the late Middle Pleistocene and the Late Pleistocene also played an important role. Starting 900,000-800,000 years ago, both the amplitude of the swing between cold and temperate climatic phases in the middle latitudes of the Northern Hemisphere and the periodicity of the climatic cycles have increased. This led

Figure 4. A late Neandertal skull and mandible (La Ferrassie 1) from western Europe (Left) compared to an Upper Paleolithic individual (Cro-Magnon 1) from the same region (southwestern France).

to the development of long cool periods, culminating in glacial episodes, alternating with shorter temperate to warm periods along cycles of about every 100,000 years (Figure 3). This development has prevailed during the last half a million years and profoundly affected the landscape, the fauna, and also the geography of the regions where hominins were evolving. In some regions, it resulted in increased isolation and major demographic fluctuations that might have amplified episodes of genetic drift.

The common origin of African *Homo sapiens*, on the one hand, and the Eurasian clade of Neandertals and Denisovans, on the other hand, has long been considered to be found among an older group of hominins assigned to the species *Homo heidelbergensis*. This latter species name was forged after the discovery of the 600,000-year-old mandible in Mauer near the town of Heidel-

berg, Germany. Unfortunately, the features that have been used to assign other specimens to this paleoanthropological species are generally not mandibular but cranial, raising questions about the validity of this denomination. *Homo rhodesiensis* has sometimes been proposed as an alternative to *Homo heidelbergensis* for the African specimens. However, the concept of *Homo heidelbergensis* remains difficult to delineate as it is likely "a root group", a sort of mixed-bag, that includes some older common ancestral forms as well as the first representatives of later diverging lineages.

A BRIEF HISTORY OF OUR AFRICAN ORIGINS

The works by William W. Howells (1908-2005) played a seminal role in the emergence of the concept of a recent common origin for all living humans. In 1973, using large samples from different regions of the world with normalized craniometric measurements, he published an extensive study of "cranial variation in man" (Howells, 1973). Howells concluded that there is a high level of anatomical similarity between the studied extant populations and a large phenotypic distance that separates them from particular groups of archaic hominins like Neandertals. According to his perspective, it was very unlikely that modern Europeans, for example, would have had a closer relationship with Neandertals living on the same continent tens of thousands of years earlier than with other living humans. This was a challenge to a central assumption of the multiregional model.

Another advance during the 1960s contradicted the hypothesis of a direct ancestor-to-descendant relationship between Neandertals and recent Eurasians. Bernard Vandermeersch and Ofer Bar-Yosef, who were excavating the site of Jebel Qafzeh in Israel, unearthed "early modern humans" that were at least as old as the European Neandertals (Figure 5) (Valladas et al., 1988; Vandermeersch,

Figure 5. A South Levantine Neandertal adult skull and mandible from Amud 1 (Israel) (Left) compared to those from the early Homo sapiens from Qafzeh 9 (Israel) (Right). In this region, the occurrence of Homo sapiens of African origin predates the latest Neandertal occupation. It is assumed that this region witnessed several episodes of gene flow between the two groups.

1966). This discovery clearly implied a long chronological overlap between the two lineages. In the following years, the reassessment and re-dating of some fossil hominins not only reinforced this picture but also highlighted the African continent and southwest Asia as regions where *Homo sapiens* appeared much earlier than in other parts of the Old World. In 1978, a young German anthropologist, Gunter Bräuer, published his views on an "Afro-European Hypothesis" for the first time. According to Bräuer's hypothesis, the origin of the European *Homo sapiens* had to be found in Africa (Bräuer, 1978; Bräuer, 1984). Following this model, their exit of the African continent was documented by the discoveries at Jebel Qafzeh and in some other sites of the Levant.
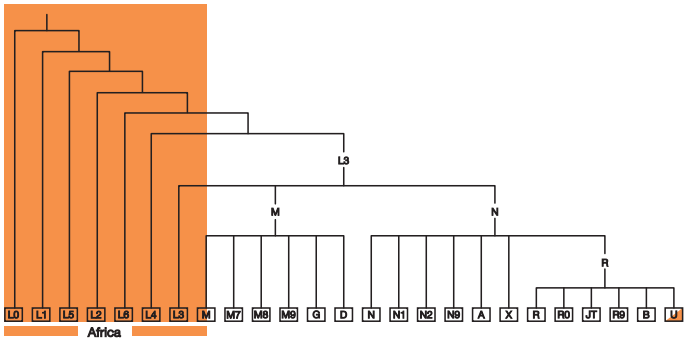
Figure 6. Simplified tree of the mitochondrial DNA lineages in extant populations of the world. The African haplotypes (highlighted in orange) display a deeper rooting and more diversity than the non-African haplotypes.

Soon, this paleontological evidence was confirmed by population geneticists. In 1987, Rebecca Cann, Mark Stoneking, and Alan Wilson published the first analysis on the variation of human mitochondrial DNA throughout the planet (Cann et al., 1987). They showed that this simple form of DNA, almost exclusively transmitted by maternal lineages without recombination, was much more diverse in the African continent than outside (Figure 6). Non-African populations represented a sub-sample of the deeply rooted African tree of lineages. The clearest way to interpret these patterns was to assume that non-African living humans all had African ancestors. Combining the fossil evidence and the genetic data, Chris Stringer and Peter Andrews formalized the currently prevailing Out-Of-Africa model (Figure 2) in a resounding *Science* publication (Stringer & Andrews, 1988). Later progress in genomics showed that the pattern of higher African diversity observed through the mitochondrial DNA was also evident with the branching of the Y-chromosome lineages. In fact, all of the subsequent studies on nuclear DNA have reinforced this model (e.g.,

Cavalli-Sforza et al., 1994). Phenotypic and genetic diversity of humans is greater in Africa and decreases outside the continent in direct relation with the distance that the ancestors of a given human population had traveled from the gate of northeast Africa across emerging lands (Figure 7) (Manica et al., 2007; Prugnolle et al., 2005).
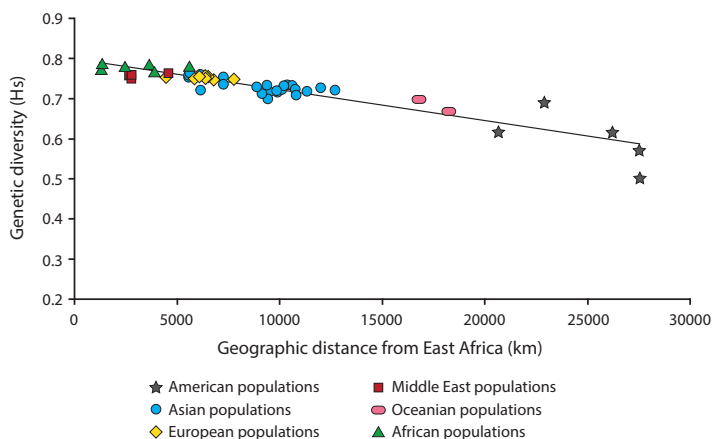
Figure 7. Genetic diversity in present day Homo sapiens from different regions of the world in relation to length of the land routes separating them from Africa. Adapted from Prugnolle et al., 2005.

The picture of the recent African origin of living populations, where modern immigrants would have totally replaced local archaic populations across Eurasia, was slightly adjusted after paleogenomic studies demonstrated that some level of assimilation of these archaic groups took place in Eurasia at the time of the replacement (Figure 8). Nostalgic believers in the multiregional models have used these new results to claim that we are now "all multiregionalists". The truth is that the contribution of the non-
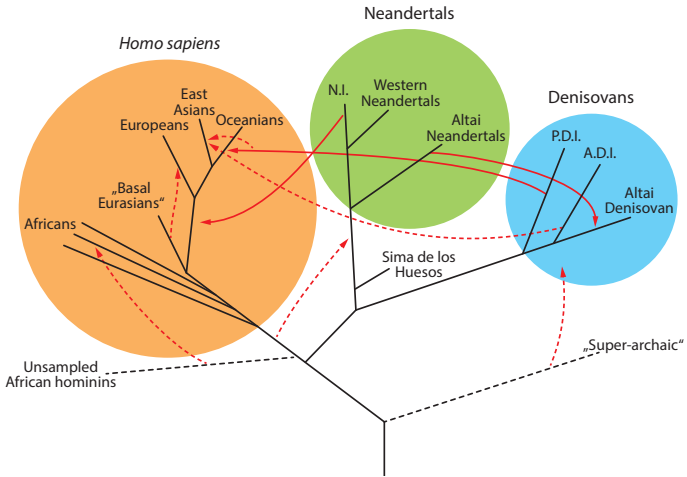
Figure 8. A schematic representation of the lineages of the three main groups of Late Middle to Late Pleistocene hominins. The solid red arrows represent main introgression events. Dashed red arrows represent introgression events that are less established. Adapted from Dannemann & Racimo, 2018.
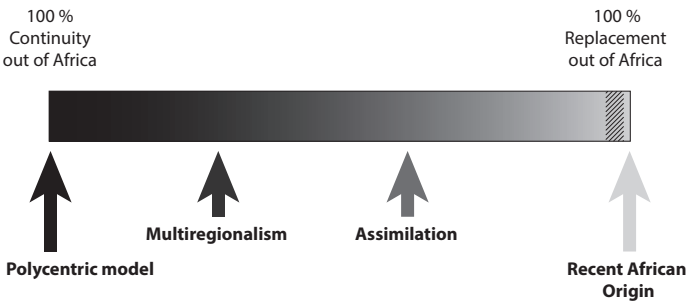

Figure 9. Compared levels of continuity of the Pleistocene populations out of Africa, according to different theoretical models. The dashed zone represents the level of archaic genetic contribution to present day humans established by the current paleogenomic data.

16

African archaic populations to the genome of living humans has been estimated to only a few percent of the DNA of a given individual – of which the magnitude of the effect on the phenotype is a matter of discussion (Figure 9).

WAS THERE A "GARDEN OF EDEN"?

Although Africa is an enormous continent in which the surfaces of western and eastern Europe, India, China, Japan, and the United States could all fit, the African hominin fossil record of the last half a million years is much smaller than that of Europe alone for the same range of time. Many discoveries occurred decades ago or outside of well-established archaeological contexts. Therefore, not only is the African record scarce, it is not always well dated either. The intensity of research efforts has also varied considerably from one part of the continent to another. This is largely due to the fact that some geological contexts are much more favorable to the preservation of fossils than others. Furthermore, the diversity of African landscapes does not always facilitate surveys. Additional issues related to historical, political, and even security factors also explain the sharp differences in terms of number of discoveries observed across borders of different countries. Africa remains a largely unexplored area from a paleoanthropological point of view, with the very noticeable exceptions of east and south Africa and, to a lesser extent, northwest Africa. Therefore, the exact time of emergence as well as the geographical location of the origin of *Homo sapiens* is largely obscured by a lack of evidence. However, chronological and geographical gaps in the fossil record have led to the simplistic notion that a restricted sub-Saharan "Garden of Eden" was the location of a rapid appearance of early modern human forms about 200,000 years ago. This picture has long been supported by a handful of discoveries in east Africa dating across the following 100,000 years, particularly those in Omo

Kibish (McDougall et al., 2005; Fleagle & Shea, 2005; Day & Stringer, 1991), Herto in Ethiopia (White et al., 2003) and Singa in Sudan (Stringer, 1979).

Various works by population geneticists have also supported the concept of a restricted Garden of Eden (e.g., Henn et al., 2011; Soares et al., 2012). However, deducing a place of origin for the ancestors of non-African *Homo sapiens* from that of living African populations is quite debatable. It assumes that most, if not all, ancient populations of hunter-gatherers still have descendants in today's world and that population movements throughout the continent were minimal or could be easily reconstructed. Both assumptions can be easily questioned. Environmental changes were paramount in the distribution and adaptation of human populations during the Middle and Late Pleistocene and, in this regard, Africa witnessed spectacular changes. Climatic cycles which were not completely synchronous with those developing in the middle latitudes of the Northern Hemisphere led to dramatic variations in the local landscapes (Drake & Breeze, 2016; Moreno, 2012). During the Pleistocene there was a general trend of increasing aridity but also episodes during which the climate briefly returned to moister conditions. Coinciding roughly with some glacial episodes in Europe, Africa experienced periods during which the rainforest extension was reduced. There were also episodes during which the Sahara was covered by vegetation, rivers, and lakes – sometimes covering a space as large as modern day Germany (Larrasoaña et al., 2013). During these "green Sahara episodes" the monsoon rainfalls, originating from the Gulf of Guinea, extended much further north than today, to around the fringes of the Maghreb (Lezine, 1991). In this vast geographical domain, numerous groups of hunter-gatherers could exploit huge areas of steppes and savannahs that would later become almost completely depopulated.

THE OLDEST *HOMO SAPIENS*

Our work in the site of Jebel Irhoud (Morocco) demonstrated that the evolutionary history of *Homo sapiens* goes much further back in time than 200,000 years and that it is not limited to an east African sub-Saharan Garden of Eden (Hublin et al., 2017; Richter et al., 2017). The cave of Jebel Irhoud is located between the towns of Marrakesh and Safi, near the top of a large hill made of Paleozoic limestone (Figure 10). In these layers, dissolution generated complex karstic networks which were filled by sediments since at least the Miocene period. In 1961, mining operations by a company exploiting baryte opened and largely destroyed a cavity close to the surface that contained remains of mammals and stone artefacts. In the course of these accidental discoveries, a human skull was found that attracted scientific attention to this site (Figure 11). In the following years, works by Emile Ennouchi and later by Jacques Tixier and Roger de Bayle des Hermens yielded the first series of hominin remains associated with lithics which were compared to those produced by Neandertals in Europe. For a long time, the interpretation of the material from Jebel Irhoud was hindered by the lack of accurate

Figure 10. The site of Jebel Irhoud (Morocco) under excavation in 2007 by the Department of Human Evolution of the Max Planck Institute of Evolutionary Anthology (Leipzig) and the Institut National des Sciences de l'Archéologie et du Patrimoine (Rabat).

Figure 11. The hominin skull of Irhoud 1. This specimen, discovered accidentally in 1961 by workers in the baryte mine of Jebel Irhoud, is the most complete skull yielded by the site to date.

dating. The hominins were initially considered to be an African version of Neandertals, and their age was estimated at slightly over 40,000-50,000 years. However, reassessments of this fossil material highlighted striking differences with Neandertals (Hublin & Tillier, 1981; Hublin, 1992). The first attempts to date the site by Electronic Spin Resonance (ESR) or U-Series methods already indicated that the initially proposed ages were strongly under-estimated (Grün & Stringer, 1991; Smith et al., 2007). However, these attempts, in the absence of an accurate dosimetry of the site, i.e. in-situ measurements of the radioactivity of the sediments forming the archeological layers, were problematic. One of the main purposes of the work undertaken in 2004 by the Department of Human Evolution in the Max Planck Institute of Evolutionary Anthropology (Leipzig) and the Moroccan Institut National des Sciences de l'Archéologie et du Patrimoine (Rabat)

was to reassess the dating of the Irhoud hominins (Figure 12). In the part of the site that was still preserved, more than three meters of archaeological deposits could be excavated. They yielded rich archeological material and new hominin remains that were essentially concentrated at the bottom of the stratigraphy. In this cave, human activities included an intense use of fire demonstrated by burnt bones and lenses of ash. Among the many flint fragments that were found, some had been exposed to fire. This opened the possibility of implementing a method that had not been used before in this site. Thermoluminescence measures the time since flint fragments were last heated. A reassessment of the ESR dates previously produced for the lower layers of this site was also possible. These two methods produced a radiometric age of around

Figure 12. Prof. Abdelouahed Ben-Ncer (Institut National des Sciences de l'Archéologie et du Patrimoine), co-director of the Jebel Irhoud project (Right), and Dr. Shannon P. McPherron (Department of Human Evolution of the Max Planck Institute of Evolutionary Anthropology), senior archaeologist (Left), at the site in 2007.

Figure 13. A reconstruction of Irhoud 11, the most complete preserved adult mandible from the site. This very large specimen combines some primitive retentions like the vertical orientation of the symphyseal profile with anatomical features shared with more recent Homo sapiens. Source: Hublin et al., 2017.

300,000 for the Irhoud hominins and their stone tools (Richter et al., 2017).

In the course of our project, the number of hominin specimens from this site increased from six to twenty-two with the discovery of a new skull, a well-preserved adult mandible, as well as dental and post-cranial elements (Figure 13). The analysis of this material by classical techniques as well as by geometric morphometrics, a method that assesses shape variations in an accurate quantitative
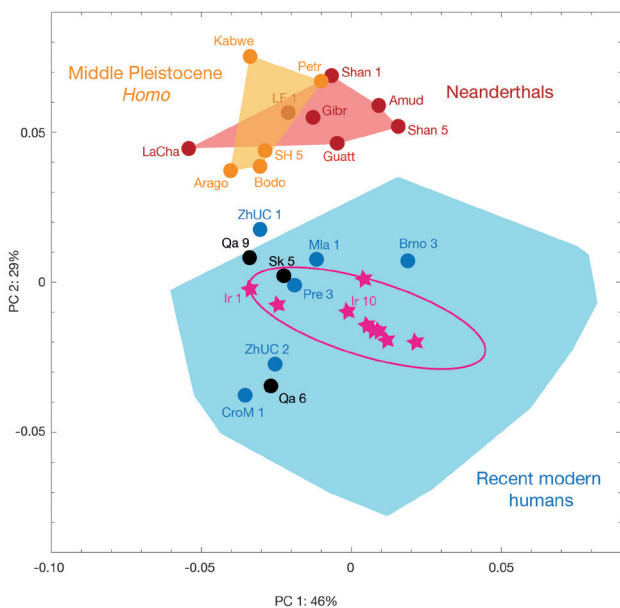
Figure 14. Comparative shape analysis (principal component analysis; PCA) of facial shape. Recent Homo sapiens are represented in blue, earlier Homo sapiens in black, Neandertals in red, and Homo heidelbergensis in yellow. The Irhoud 1 specimen as well as various possible reconstructions of Irhoud 10's face (pink) plot within variation of present day humans. Source: Hublin et al., 2017.
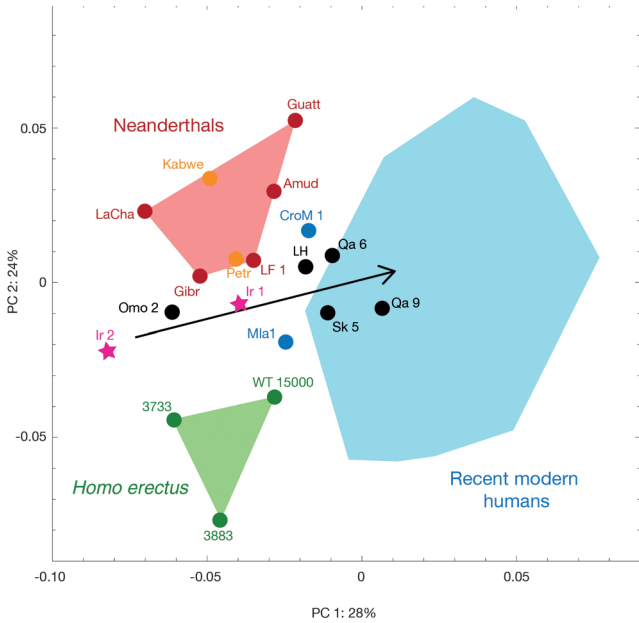
Figure 15. Comparative shape analysis (PCA) of endocranial shape. Recent Homo sapiens are represented in blue, earlier Homo sapiens in black, Neandertals in red, Homo heidelbergensis in yellow, and Homo erectus in green. The Irhoud 1 and 2 specimens (pink) plot along a black arrow that represents the evolutionary trend among early forms of Homo sapiens. Source: Hublin et al., 2017.

way, shed new light on its significance. Dental, mandibular, and facial features were reminiscent of those observed in African or Levantine specimens considered to be "early modern humans" (Figure 14). They were in sharp contrast with the pattern observed in Eurasian Neandertals. The brain cases of the two best preserved Irhoud skulls (Irhoud 1 and 2) were, on the contrary, more reminiscent of archaic hominins (Figure 15). Although their cranial capacity of around 1400 cc was comparable to that observed in

extant humans, the shape of the endocast (the internal cavity of the skull that is directly related to the brain shape) did not display the globular pattern found in recent *Homo sapiens*. Instead, it was longer and broader (Hublin et al., 2017). This mosaic of features demonstrates that the Irhoud hominins represent a primitive form of *Homo sapiens* predating the emergence of a fully "modern" morphology.

Further analysis of the shape of the endocasts from Pleistocene hominins showed that brain evolution over most of the last 2 million years is characterized by an increase in size without major shape changes (Figure 16) (Neubauer et al., 2018). In contrast, representatives of *Homo sapiens* depart from this evolutionary trend by acquiring a more globular brain shape. Starting with the specimens from Jebel Irhoud, without much changes in terms of brain volume, one sees *Homo sapiens* brains evolving in a totally different direction than that followed by *Homo erectus* and Neandertals. Importantly, this evolution seems to have been gradual as it is only between 50,000-100,000 years ago that the brain shape of fossil *Homo sapiens* entered the variability of extant humans. This gradual pattern strongly questions the validity of a well-defined "anatomically modern stage" in the latest steps of *Homo sapiens* evolution. The globularization of the brain in our species essentially relates to a bulging of the parietal lobes without much increase of their cortical surface (Figure 17). This bulging is likely the result of changes to an underlying internal cerebral structure. Another spectacular development relates to the increase of the size of the *cerebellum*, a part of the brain that encompasses more than half of our neurons. The *cerebellum* is involved in motor coordination but also in speech production, control of the reward circuitry, and social behavior (Carta et al., 2019). It is also likely that connectivity of the brain was improved during this evolution. This is suggested by the identification of non-synonymous mutations in *Homo sapiens* lineages affecting some genes involved in brain
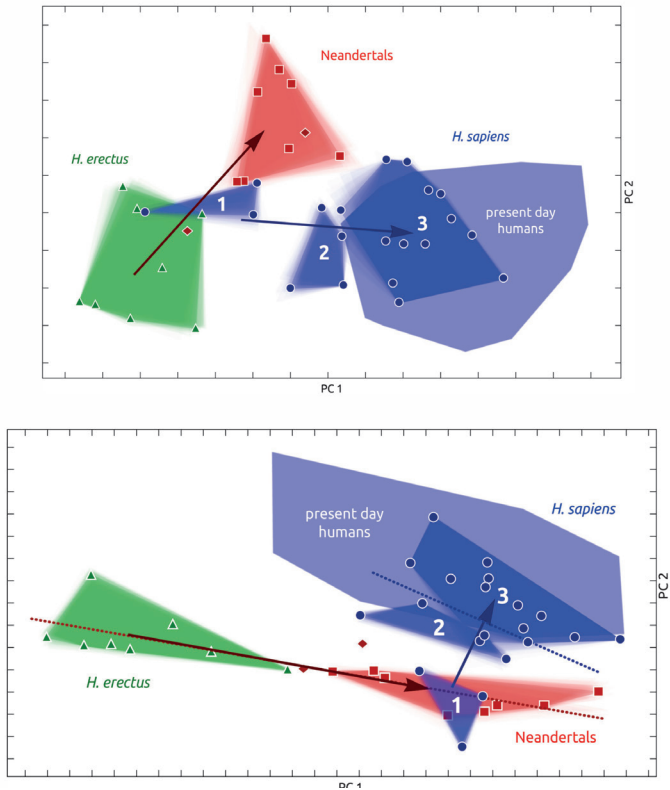
Figure 16. Comparative shape analysis (PCA) of endocranial shape (Top). Comparative form analysis (PCA) incorporating a size factor of endocranial shape (Bottom). Successive chronological groups of humans (numbered 1-3) are represented by purple polygons. Neandertals are represented in red and Homo erectus in green. Source: Neubauer et al, 2018.

development and functioning (Prüfer et al., 2014). Importantly, differences between regulatory parts of the genomes of *Homo sapiens* and archaic hominins might have had an even greater critical impact on their capabilities (Petr et al., 2019).

The discoveries of Jebel Irhoud not only pushed the first occurrence of *Homo sapiens* in the fossil record much further back in time, but also opened entirely new perspectives on the geographic distribution of the species. Paleogeneticists estimate that the split between the Eurasian clade of Neandertals and Denisovans and groups ancestral to *Homo sapiens* took place between 550,000-765,000 years ago (Meyer et al., 2016). There is likely a long history of our species predating the humans from Jebel Irhoud that we still have yet to decipher. To date, it remains very difficult to
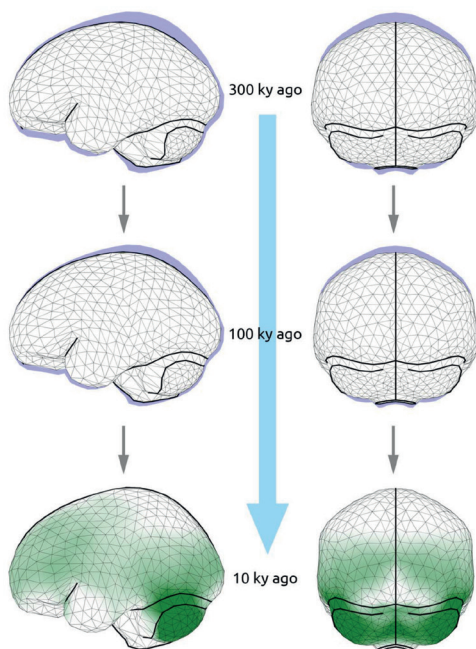
Figure 17. Globularization of the brain in Homo sapiens during the course of the last 300,000 years. Shape changes are highlighted in green. Source: Neubauer et al., 2018.

identify a region of origin in Africa but clearly the earliest stages of *Homo sapiens* evolution did not take place exclusively in east-Africa.

Figure 18. Early Middle Stone age stone tools from the hominin layers of the Jebel Irhoud cave site. The assemblage is characterized by the use of Levallois debitage and the high frequency of points and convergent side scrapers. Source: Richter et al, 2017.

Figure 19. A map of the main early Middle Stone Age sites of Africa. The occurrence of hominin fossils are highlighted in red. Source: Shannon McPherron.

The stone tools associated with the Jebel Irhoud hominins are assigned to one of the oldest forms of the Middle Stone Age (Figure 18) (Richter et al., 2017), a type of lithic assemblage following Acheulean industries in Africa. Similar ancient Middle Stone Age assemblages appeared roughly at the same time in east and south Africa (Figure 19). As such, it is tempting to relate this emergence to the spread of our species. Noticeably, one of the longest green Sahara episodes of the Middle Pleistocene took place just before 300,000 years ago. It facilitated exchanges of human and animal populations between north Africa and the rest of the continent.

Two fossils that are unfortunately not very well dated, found in Eliye Springs (Kenya; Bräuer & Leakey, 1986) and Florisbad (South Africa; Grün et al., 1996), are reminiscent of the Jebel Irhoud hominins in regard to their anatomical features. Archaeological and paleontological evidence therefore suggest that around 300,000 years ago, early forms of *Homo sapiens* were already spread all over the continent. This expansion, wherever it started, largely predates the appearance of *Homo sapiens* populations that some have called "modern". This finding supports the view that the populations of several African regions might have played a role in the constitution of present-day humankind. An emerging Pan-African model for the evolution of *Homo sapiens* posits that the succession of periods of aridity and green Sahara episodes resulted in a series of regional isolation phases alternating with periods of exchange between populations of advantageous genetic mutations and cultural innovations. It has even been proposed that a sort of "in-Africa multiregionalism" took place (Scerri et al., 2018; Schlebusch et al., 2017). However, based on the current fossil evidence, the persistence of evolutionary continuity within given African regions over more than 300,000 years is, to say the least, difficult to substantiate. The magnitude of the environmental changes during this span of time might well have re-shuffled the population structure of the continent several times.

An intriguing and stimulating aspect of the morphometric analysis of the Jebel Irhoud material is the challenge it poses for the conventional interpretation of *Homo heidelbergensis* as the common ancestor of Neandertals and *Homo sapiens*. Based upon the evolution of the face, as well as of the braincase, the specimens assigned to this taxon appear far too derived in their own direction to represent an ancestral form for *Homo sapiens*. Their grouping with the Neandertals does not come as a surprise for the Eurasian specimens of Petralona (Greece), Arago XXI (France), or Sima de los Huesos 5 (Spain). It is, however, more problematic for the

African fossils of Bodo (Ethiopia) and Kabwe (Zambia). This raises the possibility that the latter could belong to an African population close to the Neandertal/Denisovan ancestry but unrelated to *Homo sapiens* (Figure 3). Hopefully, further discoveries will allow us to entertain the hypothesis that a group of archaic hominins, maybe of Eurasian origin, could have been present in some parts of the African continent in addition to the earliest forms of *Homo sapiens*.

OUT OF AFRICA

There have been several hypotheses proposed to explain the reasons for the movement of *Homo sapiens* out of Africa (Klein, 2009). This dispersal might be related to intrinsic factors which affected the reproductive success, fitness, and demography of African hunter-gatherer populations at that time. It could also be a consequence of environmental changes that created conditions for the expansion of these African groups into southwest Asia and later all over Eurasia. The most popular of these models relates the presence of ancient forms of *Homo sapiens* in southwest Asia with the development of green Sahara episodes (Timmermann & Friedrich, 2016). During this period of relative moisture in the climate, the desert belt ranging from the Atlantic Ocean to the Persian Gulf became favorable to the settlement of hunter-gatherers. In a landscape of semi-desert areas surrounded by steppes and arboreal savannah, these populations could prosper not only in a large portion of north Africa, but also in the Arabian Peninsula. Under such conditions, they could have passively dispersed out of Africa into areas that were at the southern fringes of the Eurasian domain of Neandertals. Such an episode could have even occurred around the time of the Jebel Irhoud hominins. Inconsistencies between the molecular phylogenies established on mitochondrial DNA and on nuclear DNA support the hypothesis of an introgression

of mitochondrial DNA of African origin into the genome of early Neandertals (Posth et al., 2017). This event could have taken place in a window of time between 220,000-470,000 years ago and would explain why Denisovans and early Neandertals display a different type of mitochondrial DNA than later Neandertals.

In the fossil record, the first known occurrence of *Homo sapiens* in the Levant is documented by the discovery of a 180,000-year-old human maxilla in the cave of Misliya (Israel; Hershkovitz et al., 2018). Various archaeological arguments have also been provided to advocate for the presence of early forms of *Homo sapiens* in the Arabian Peninsula (Crassard et al., In Press; Rose & Marks, 2014). Yet, the anatomical evidence is still very sparse (Groucutt et al., 2018). In the south of the Levant, the sites of Skhul and Qafzeh (Israel) provided abundant evidence of this presence close to the gate of Africa and to the Arabian Peninsula during the last interglacial period, between 130,000 to 90,000 years ago (Grün et al., 2005; Mercier et al., 1993; Valladas et al., 1988).

The timing of the colonization of South Asia by our species is a matter of intense debate. It is claimed that humans reached Australia before 60,000 years ago (Clarkson et al., 2017) and, therefore, they must have been present in southeast Asia before this date. The cave of Tam Pa Ling (Laos) and its human remains probably provide the most convincing evidence of this presence in tropical southeast Asia about 70,000 years ago (Demeter et al., 2017). However, further north, there have also been claims for the presence of *Homo sapiens* in southern China as early as 100,000 years ago (Liu et al., 2015).

Noticeably, the arrival of so-called modern humans into the middle latitudes of Eurasia did not occur until much later. Arguably, the dispersal of these tropically adapted populations into southern Asia was easier than into the Eurasian temperate or cold environ-

ments. Forty-five thousand years ago, a human femur from Ust'-Ishim in western Siberia demonstrates that migrants with African origins had already developed the technical capabilities to adapt to above 50 degrees in the northern latitudes. This spread can be connected to the development of new technocomplexes assigned to the Initial Upper Paleolithic from 47,000 years onward. These industries mixed a Middle Stone Age heritage and technical innovations that would further flourish in the later Upper Paleolithic. They seem to be rooted further south in the Emirian techno-complexes of the Levant such as that of Boker Tachtit in the Negev (Skrdla, 2003). These industries are found over a wide geographical domain, going from eastern Europe (Figure 20) through central Asia until reaching the Altai. The sites of Üçağızlı Cave (Turkey) or Kara-Bom (Altai) yield body ornaments made of shells and mammalian hard tissues (Stiner et al., 2013; Zwyns et al., 2012). Genetic evidence suggests that these pioneer populations have very few – if any – descendants in present day Europeans or Asians.

The second wave of dispersal coming from southwest Asia can be tracked across Europe by the expansion of the Aurignacian complex a couple of millennia later (Hublin, 2015). These later groups, which are part of the ancestry of present-day Europeans, reached the far west of Europe and replaced the last Neandertals. Therefore, current evidence indicates that this process of replacement and partial assimilation of one species by another took at least 6 to 8 millennia at the European scale. Well-adapted Neandertal populations had been quite resilient for a long period of time, but, to date, there is no evidence of a local coexistence of the two groups for any significant length of time. Yet, the sharing of territory in this part of Eurasia at different stages of this process is still to be established. Some level of gene flow took place and most likely some form of acculturation at distance by stimulus diffusion deeply influenced the evolution of the last Neandertals in western Europe.

Legend:
- Emirian/Bachokirian/Bohunician
- Early Ahmarian/Kozamikian/Protoaurignacian
- Early Aurignacian
- Uluzzian
- • • • • Szeletian
- – – – – MTA
- ——— Châtelperronian
- –·–·– Lincombian/Ranisian/Jermanowician
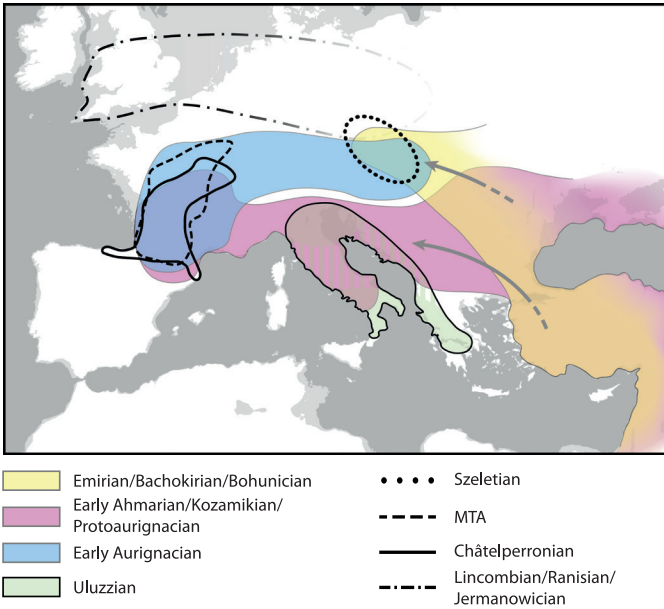
Figure 20. Geographical distributions of the main lithic assemblages of Western Eurasia between 50 and 35 ka cal BP. With the exception of the Mousterian of Acheulean tradition (MTA), the late Middle Paleolithic industries produced by Neandertals are not represented. Emirian/Bachokirian/Bohunician likely represent technocomplexes produced by an early wave of Homo sapiens. It was followed by the dispersal of the makers of Aurignacian industries who replaced the last Neandertals. A set of "transitional assemblages," such as the Châtelperronian, might have been produced by the latest Neandertal populations.

One of the greatest challenges that paleoanthropology has faced for several generations is the finding of a comprehensive explanation for this final replacement which is arguably the most important episode of hominin evolution. It led to the supremacy of a single species over all of the territories formerly peopled by a variety of archaic hominins. Ultimately, previously uninhabited territories like the colder lands of Eurasia and, later, the American continents were colonized. Not only were local populations like the Neandertals replaced, but the last 100,000 years also witnessed a large number of mammalian extinctions especially in continental areas where the fauna had not experienced a long co-evolution with *Homo sapiens*. The outstanding ability of *Homo sapiens* to exploit new environments was probably not just based on its technical capabilities. In this domain, Neandertals had been able to develop far more complexity than previously thought. The strength of social networking at different geographical scales and the emergence of well differentiated and cohesive cultural units unified by the sharing of common beliefs might be key features of the latest forms of *Homo sapiens* that contributed to their success.

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