Mapping Interactions of *Homo neanderthalensis* and *Homo sapiens* From the Fossil and Genetic Records

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submitted: 11 July 2022; revised: 7 September 2022; second revision: 11 September 2022; accepted: 11 September 2022

ABSTRACT

Genetic evidence suggests that the Neanderthal and *Homo sapiens* lineages began diverging about 600 ka ago, evolving largely separately in Eurasia and Africa after that time. Around 60 ka ago, *H. sapiens* began an important emergence from Africa that would lead to a near-global distribution by 10 ka ago. Until recently, there were few other signs of a *H. sapiens* presence in Europe prior to the Aurignacian expansions that began around 41 ka ago. However, recent research on fossils from Apidima Cave (Greece) suggests that there was an earlier dispersal of our species that reached Europe more than 200 ka ago, which is consistent with data from ancient DNA suggesting gene flow between the early *H. neanderthalensis* and *H. sapiens* lineages during the time span of the later Middle Pleistocene. Additionally, new data from sites like Zlatý kůň (Czechia), Bacho Kiro Cave (Bulgaria), Grotta del Cavallo (Italy) and Grotte Mandrin (France) indicate that there were pre-Aurignacian dispersals that potentially placed *H. sapiens* populations alongside the persisting Neanderthals. While some of these populations can be related to later Eurasians, others seem to represent now-extinct lineages of *H. sapiens*. Furthermore, it is now known from a growing body of genetic data that this co-existence of *H. neanderthalensis* and *H. sapiens* was accompanied by bouts of interbreeding between the two species. This paper reviews the growing evidence for early dispersals of *H. sapiens* into Europe and discusses how these populations might have interacted with each other, and the social backdrop of these genetic exchanges. It is suggested here that a continuing absorption of Neanderthal individuals into *H. sapiens* groups could have been one of the factors that led to the demise of the Neanderthals.

INTRODUCTION

Only a few years ago it was still possible to argue that even though *H. sapiens* began to disperse from its ancestral African homeland at least 60 ka ago, the arrival of our species in Europe took much longer, perhaps only occurring with the arrival of Aurignacian industries about 41 ka ago (Banks et al. 2013). This delay was hypothesized to have been caused by the need to develop adaptations to colder European environments, or possibly because the resident human species *H. neanderthalensis* successfully excluded *H. sapiens* for many millennia (Stringer 2011). However, since 2019 there has been a succession of publications that demonstrate a longer-term potential co-existence of early *H. sapiens* and late Neanderthals not only in western Asia, as previously observed, but also in Europe. Moreover, ancient DNA evidence shows that this overlap was accompanied by multiple episodes of interbreeding between these populations, in Europe as well as in Asia.

In this paper, we will first consider the species status of *H. sapiens* and *H. neanderthalensis* and the use of terms like ‘archaic,’ ‘modern,’ ‘early,’ and ‘late’ in differentiating evolution along their lineages. We will then briefly examine what is known about the development of the Neanderthal and *H. sapiens* lineages in Eurasia and Africa, respectively, and review the growing evidence for early dispersals of *H. sapiens* into Eurasia. Next, we will focus on the period between 40–60 ka in Europe, and emerging evidence for multiple arrivals of *H. sapiens* populations, associated with different lithic technologies. Finally, we will consider how Neanderthal and *H. sapiens* groups might have regarded each other and the social milieu through which they exchanged genes, and anticipate new data that will enrich our understanding of the complex interactions between these ancient populations.

***P**aleo**A**nthropology* **2022:2: 401–412. https://doi.org/10.48738/2022.iss2.130 ISSN 1545-0031**
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HOMO SAPIENS AND *HOMO NEANDERTHALENSIS*

Most paleoanthropologists regard Neanderthals and *H. sapiens* as distinct species of humans (*H. neanderthalensis* and *H. sapiens*, respectively). The physical traits of our species include a high and rounded ('globular') braincase, a small and divided brow ridge, and a relatively narrow pelvis, while the Neanderthals exhibit a relatively longer, lower skull, a large continuous brow ridge, and wider, more flared hipbones. Even the three small bones of our middle ear, vital in hearing, can be readily distinguished from those of Neanderthals with careful measurement. Furthermore, several studies have shown that Neanderthal-*sapiens* differences in features such as cranial and ear bone shape match or exceed those found in distinct species of primates (Harvati 2003; Harvati et al. 2004; Stoessel et al. 2016). Thus, there is enough physical evidence to classify us as a different species from the Neanderthals, and genetic data indicate that our lineages began to go their separate ways more than 500 ka ago (Hajdinjak et al. 2018; Meyer et al. 2016) or even earlier (e.g. Gómez-Robles 2019; Ni et al. 2021). However, we now know that this separation was not sufficient to prevent interbreeding between these evolving populations (e.g., Green et al. 2010; Nielsen et al. 2017; Sankararaman et al. 2016; Vernot et al. 2016), something also observed in many closely related species today (Taylor and Larson 2019).

Demarcating evolution along the Neanderthal and *H. sapiens* lineages requires additional terminology, but there are some fundamental and difficult nomenclatural issues that have dogged discussions of recent human evolution for many years—the terminology used around "archaic" and "modern" humans. Many researchers use the latter term in both popular and academic discussions to represent the "anatomically modern" skeletal morphology of recent and extant *H. sapiens* who, as mentioned already, share specific traits such as a high neurocranium, rounded in lateral profile, a small face retracted under the frontal bone, a true chin even in infants, a small and discontinuous supraorbital torus, a lengthened post-natal growth period and life history, and a narrow ribcage, trunk, and pelvis (trait list modified from Stringer 2016). However, one of us (CS) recently proposed that '[anatomically] modern humans' is too confusing a term, as it is used in too many different ways and regularly gets conflated with 'recent humans,' 'extant humans,' and 'behaviorally modern humans'—terms that have their own problems of definition. The invariably linked term 'archaic' also results in a contradictory situation where Neanderthals are described as 'archaic' humans (because they are not 'modern' human), even though they have numerous derived traits, such as a large brain, projecting midface, and distinctive ear bones. One of us (CS) has addressed this confusion by sometimes using the alternative terms 'early' and 'late' for *H. sapiens* fossils. However, many of the remains to which these terms were applied are undated or have disputed dating; and moreover, the age of a fossil does not necessarily indicate how plesiomorphous or derived its morphology is.

CS discussed these issues on social media in April 2021 and received much useful feedback and ideas. For instance, Mike Plavcan suggested simply using the terms 'basal' (showing traits close to the ancestral position on a tree or phylogeny) and 'derived' (meaning having specialized, non-ancestral traits), which also are not characterized by the social baggage that comes with using a word like 'primitive' in common parlance. Both these words have had wide usage in phylogenetic discussions, though much more limited in paleoanthropology (but see Strait 2013).

According to this solution, we could therefore say that fossils like Jebel Irhoud 1 and Omo Kibish 2 represent basal *H. sapiens* (bHs), while on the parts preserved Omo Kibish 1 could be described as a derived *H. sapiens* (dHs). Equally, early members of the Neanderthal lineage such as those from the Sima de los Huesos could be called basal Neanderthals (bHn), while fossils like La Ferrassie 1 and Forbes' Quarry would be referred to as derived Neanderthals (dHn). Scrapping the 'archaic' vs. 'modern' dichotomy would also end the vague labelling of 'archaic' introgression, which means we can be more specific in talking about Neanderthal-lineage introgression, Denisovan-lineage introgression, non-Hs lineage introgression, etc. However, feedback on social media pointed out that terms like basal and derived are relative, and questioned who gets to decide which to use. To this, it could be argued that the same (or worse) problem applies to the terms 'archaic' and 'modern.' Furthermore, even when using 'basal' and 'derived' informally, it should at least be possible to refer to a phylogeny or a list of traits to clarify how these decisions were made. After all, relative terms like 'large' and 'small' and 'hot' and 'cold' are used all the time, but they are useful, nonetheless. It is hoped that the same can apply to 'basal' and 'derived' when human fossils are discussed.

NEANDERTHALS EVOLVED IN EUROPE FOR AT LEAST 400 KA YEARS

The Sima de los Huesos ('pit of the bones'; SH) cave chamber in the Atapuerca hills of northern Spain is famous for the many partial skeletons of early humans it contains, dating from about 430 ka (Arnold et al. 2014; Arsuaga et al. 2014). Analyses of these bones and teeth suggested that they could be early relatives of the Neanderthals, and this conclusion was supported in 2016 when ancient DNA was recovered from one of the SH fossils, placing it on the Neanderthal lineage (Lacruz et al. 2015; Meyer et al. 2016). When these genetic data are combined with genomes from later Neanderthals and dHs, they suggest that a divergence between the Neanderthal and *H. sapiens* lineages began about 600 ka ago. This, combined with new research discussed below, has led to a change in thinking concerning who the last common ancestor (LCA) of Neanderthals and *H. sapiens* was. Previously, many researchers accepted that the LCA was the earlier species *H. heidelbergensis/rhodesiensis*, represented in Europe by fossils such as Petralona (Greece) and Arago (France), and in Africa by Bodo (Ethiopia) and Kabwe [Broken Hill 1] (Zambia) (Rightmire 1998; Stringer 1983, 2012). This species would have started to split about

500 ka ago, and then gradually give rise to the Neanderthals in Eurasia and modern humans in Africa. However, recent dating work on the Kabwe cranium of *H. rhodesiensis* has shown that this specimen could be dated to only about 300 ka, much younger than the expected age for an ancient African ancestor of ours (Grün et al. 2020). Moreover, recent studies of the facial shape of *H. rhodesiensis* fossils suggest that they have a derived zygomaxillary morphology, and thus they are less likely to represent our ancestors (Lacruz et al. 2019). Therefore, in our view, there is currently not enough evidence to establish the exact nature of our LCA with the Neanderthals from about 600 ka, nor where it lived.

HOMO SAPIENS EVOLVED IN AFRICA OVER THE SAME TIME SCALE AS NEANDERTHALS EVOLVED IN EURASIA

However, if our line of evolution stretches back to about 600 ka, where are the equivalents of the SH fossils that should document the early evolution of our species? Until recently, many scientists argued that the human fossils Omo Kibish 1 and Herto BOU-VP-16/1 from Ethiopia, dated between about 150–200 ka, represented the earliest known members of our species, *H. sapiens* (Aubert et al. 2012; Brown et al. 2012; McCarthy and Lucas 2014; McDougall et al. 2005; White et al. 2003). Both these fossils have globular braincases and reduced brow sizes, and Omo Kibish 1 has been also shown to have a *sapiens*-like hipbone (Hammond et al. 2017), as well as a greater antiquity than estimated previously (Vidal et al. 2022). If these Ethiopian specimens represent dHs, there seems to be a large temporal gap between them and our much more ancient common ancestor with the Neanderthals. It has been argued that other African fossils, such as Florisbad (South Africa) and Eliye Springs (Kenya), might represent more plesiomorphous *H. sapiens* populations that existed earlier on our lineage, but the evidence is incomplete and not well-dated (Stringer 2016). In 2017, two studies were published describing old and new fossil and archaeological discoveries from Jebel Irhoud, Morocco, dating the material found there to about 300 ka (Hublin et al. 2017; Richter et al. 2017), much older than previously proposed dates (Grün and Stringer 1991; Smith et al. 2007). These finds show features indicating they could represent early members of the *H. sapiens* lineage, shifting northern Africa from a supposed backwater in the evolution of our species to a more prominent position. The Jebel Irhoud fossils display some ancestral features such as a longer, lower braincase, strong brow ridges, and a large face and teeth, as one might expect at around 300 ka. Yet, the delicate cheekbones and retracted face look more derived, as do details of the skulls and teeth, and the shape of the jawbones. Associated evidence of the controlled use of fire and the sophistication of the stone tools from Jebel Irhoud also suggest complex behaviors in these putative early members of our lineage.

Other discoveries suggest that the Jebel Irhoud people were not alone in Africa about 300 ka ago, and their place in the evolution of our species is not a straightforward one. It now seems likely that at least three human species existed across the African continent at that time. While the lineage of *H. sapiens* was probably present in Morocco, as discussed above, it now seems that *H. rhodesiensis* persisted at Kabwe in Zambia (Grün et al. 2020). Additionally, it is now known from hundreds of fossils found deep in the Rising Star cave system near Johannesburg that a much more plesiomorphous species called *H. naledi* existed in southern Africa at that time (Berger et al. 2015; Bolter et al. 2020; Dirks et al. 2015; Hawks et al. 2017). More complications come when the Jebel Irhoud finds are compared with other fossils assigned by some workers to early *H. sapiens* from sites like Eliye Springs and Guomde (Kenya), Florisbad (South Africa), Omo Kibish 2 (Ethiopia), and Ngaloba (Stringer 2006, 2016). These show great variation and different combinations of ancestral and more derived traits, which do not suggest an orderly, sequenced evolution of dHs features, or may even question their assignment to the *H. sapiens* lineage (Mounier and Mirazón Lahr 2019). Instead, one of us (CS) and several other researchers now favor a more complex pan-African model for the evolution of our species, where our ancestors were diverse in form and scattered across much of the African continent (Hublin et al. 2017; Scerri et al. 2018; Stringer 2002, 2016). Influenced by ever-changing climates, regional lines of evolution waxed and waned, sometimes reticulating, sometimes going their separate ways, and sometimes disappearing altogether. What are called 'modern humans' are the eventual result of a blending of these different ancestral populations over a period of hundreds of thousands of years in Africa.

EARLY DISPERSALS OF *HOMO SAPIENS* FROM AFRICA

DHs started a significant dispersal from Africa about 60 ka ago (Bergström et al. 2021; Liu et al. 2021) and Neanderthal populations disappeared about 20 ka later (Higham et al. 2014). Were those two events connected, and what happened when the two species met? New discoveries in the archaeological, fossil, and genetic (ancient DNA) records are starting to reveal connections between the two populations 40–60 ka ago, including numerous interbreeding events (Fu et al. 2014, 2015; Green et al. 2010; Hajdinjak et al. 2021; Hublin et al. 2020; Prüfer et al. 2014, 2021).

Although the evolution of Neanderthals and dHs seems to have proceeded largely separately in their respective regions, ancient DNA evidence has recently emerged that they may have exchanged some genes about 250 ka ago, perhaps when early *H. sapiens* made brief forays into Eurasia (Petr et al. 2020; Posth 2017). The spread of prepared core technology around this time might reflect such contact, and fossil remains that could also mark an excursion from Africa have been found at Apidima Cave in Greece, where the back part of a *sapiens*-like braincase has been dated to at least 210 ka (Harvati et al. 2019). When the two fossil human crania from Apidima Cave were first studied, their close proximity within the deposits led to the assumption that the Uranium Series determination conducted on Apidima 2, which yielded an age of at least 160 ka, applied to both of them. The more complete Apidima 2 cranium showed shape similarities to Neanderthal crania like La Chapelle-aux-Saints (France), but further studies of the (previously unpublished) Apidima 1 partial cranium showed fewer similarities with Apidima 2 and Neanderthal fossils than expected, with features closer to those observed on *H. sapiens* fossils from the last 130 ka.

The results from new dating analyses were unexpected, placing Apidima 2 at a minimum of 170 ka and Apidima 1 at a minimum of 210 ka, and morphometric comparisons showed that on the parts preserved, Apidima 1 exhibits features typical of dHs. Although the Apidima 1 cranium is incomplete and its shape is partly based on mirror-imaged reconstruction, the multiple tests performed on the reconstruction and the large comparative dataset used increased the resolving power of the analyses, suggesting with relative confidence that Apidima 1 presents a high and rounded back to the skull that is typical only of *H. sapiens*. Both fossil crania were directly dated by the Uranium series method, which generally provides a minimum age when used on bones. In contrast, the consolidation of the hardened matrix between the crania can be dated to about 150 ka, consistent with the subsequent fossilization process. These results suggest a new scenario whereby there was an early *H. sapiens* population in Greece by 210 ka, perhaps related to comparable groups in the Levant, and which was subsequently replaced by a Neanderthal population by about 170 ka.

If the Apidima analyses are correct (for an alternative view see Rosas and Bastir 2020), *H. sapiens* entered Europe over 150 ka earlier than previously thought, raising a whole new range of questions and possibilities, including where they came from, and what happened to them. The most likely route from Africa would have been through the Levant and Turkey. The existence of such early *H. sapiens* groups outside Africa is indicated, as already mentioned, from signs of early DNA exchanges between Neanderthal and *H. sapiens* populations, when comparing the older time scale for their LCA based on genomic data, and the younger time scale derived from mtDNA and Y-chromosome analyses (Petr et al. 2020; Posth et al. 2017). Unfortunately, there are no stone tools directly associated with either of the Apidima crania to help in establishing archaeological connections elsewhere; but the Apidima evidence implies that the handiwork of these early *H. sapiens* must be present in the European record of the later Pleistocene.

There are certainly signs of other early excursions of *H. sapiens* from Africa as indicated by remains in Israel from sites like Skhul, Qafzeh, and Misliya dating from over 100 ka (Grün et al. 2005; Hershkovitz et al. 2018; Stringer 2016) (Figure 1). It has been recognized for many years that the Skhul and Qafzeh remains, which we regard as dHs, date from about 100–130 ka (Stringer 2016), and in 2017 a partial upper jaw with a complete series of teeth on the left side was published from Misliya Cave, and assigned to derived *H. sapiens*, with a minimum age estimate of ~174 ka (Hershkovitz et al. 2018). Since then, some more Neanderthal-like fossils, including a partial mandible and braincase, have been recovered and published from the site of Nesher Ramla in Israel (Hershkovitz et al. 2021), suggesting that there was substantial late Middle Pleistocene human variation in the region, including potential co-existence of members of the *H. sapiens* and *H. neanderthalensis* lineages. There is also evidence beyond western Asia and Europe for dispersals of dHs prior to 60 ka in regions ranging from southern China to Sumatra to northern Australia (Clarkson et al. 2017; Liu et al. 2015; Westaway et al. 2017), although not everyone is convinced by the data (O'Connell et al. 2018). Nevertheless, analyses of extant genomes outside of Africa suggest that the main dispersal of *H. sapiens* started about 60 ka ago (Bergström et al. 2021; Liu et al. 2021), and the subsequent disappearance of the Neanderthals about 20 ka later could well relate to that event. However, this end was only a physical one, in the sense that skeletons with Neanderthal traits disappear from the fossil record. This is because the recovery of ancient DNA over the last decade or so has shown that Neanderthals interbred with early dHs before they vanished (Green et al. 2010; Sankararaman et al. 2016), meaning that most people living outside of Africa have around 2% of Neanderthal DNA in their genomes.

In addition to the physical remains of early dHs, archaeologists also use the traces these people left behind in the form of material culture, such as stone tools, to trace their range expansions from Africa. The material cultures grouped together as Upper Paleolithic have proved important in mapping the early spread of dHs in western Asia and Europe, and until recently there were few signs of a *H. sapiens* presence in Europe prior to the Aurignacian expansions that began around 41 ka ago (Haws et al. 2020). There were earlier and enigmatic stone tool industries described as transitional (because they showed mixed features of the Middle and Upper Paleolithic), such as the Uluzzian in Italy; and others described as Initial Upper Paleolithic, such as the Bachokirian from Bacho Kiro in Bulgaria, where the nature of the manufacturers had not been established (Hublin 2015). However, in the last few years, important new evidence has emerged from sites like Bacho Kiro Cave in Bulgaria, Zlatý kůň Cave in Czechia, Grotta del Cavallo in Italy, and Grotte Mandrin in France, that seemingly push that arrival date even further back (Hublin et al. 2020; Moroni et al. 2018; Prüfer et al. 2021; Slimak et al. 2022). Additionally, beyond Europe but without archaeological associations, a partial human femur from a male *H. sapiens* individual was discovered at Ust'Ishim (Omsk Oblast, Russian Federation), dated to ~45 ka, and whose genome sequence indicated Neanderthal gene flow into his ancestors about 7–13 ka before he lived (Fu et al. 2014).

The transitional industry known as the Uluzzian is recorded from several sites in Italy dated between about 40–45 ka (Douka et al. 2014), and there has long been debate about whether its manufacturers were late Neanderthals or early *H. sapiens*. However, in 2011 two deciduous teeth from Grotta del Cavallo were identified as representing *H. sapiens* based on their morphology (Benazzi et al. 2011), a key discovery in revealing a previously unidentified spread of *H. sapiens* through the northern Mediterranean region. Unfortunately, no ancient human DNA from any of

Figure 1. A map showing some of the key localities mentioned in this paper. In particular, it shows the European sites of early H. sapiens *discussed here, together with La Cotte de St. Brelade, and relevant chronologies (map made with Natural Earth. Free vector and raster map data available at naturalearthdata.com).*

the Uluzzian sites has been recovered yet.

The Zlatý kůň partial skull and skeleton were discovered in 1950 in a cave with Upper Paleolithic tools, and at the time thought to be only about 15 ka old (Rmoutilová et al. 2018; Svoboda 2000). However, new analyses of this female skull have recovered ancient DNA suggesting the remains could be ~45 ka old (Prüfer et al. 2021). Her genome suggests that she predated the divergence of today's European and Asian populations, and it contains relatively large segments of Neanderthal DNA from a preceding interbreeding event.

The finds from Bacho Kiro, dated to between about 46–42.5 ka, paint a slightly different picture of an early *H. sapiens* population in eastern Europe. There, three tooth and bone fragments associated with the Initial Upper Paleolithic Bachokirian industry have yielded DNA indicating that these individuals had Neanderthal ancestors only a few generations back (Hajdinjak et al. 2021). The recency of Neanderthal ancestry is similar to that estimated for the ~37–42 ka old Oase 1 individual from Romania (Fu et al. 2015), but whereas the Oase male was unrelated to later Eurasians, the Bacho Kiro genomes showed links to East Asians (Hublin et al. 2020), including the ~40 ka old skeleton from Tianyuan Cave, China (Fu et al. 2013). This hints at an early Eurasian dispersal of *H. sapiens* that either occurred after the time of the Zlatý kůň female and Ust'Ishim male, or was a completely separate event (Hajdinjak et al. 2021). What is also remarkable about the Bacho Kiro evidence is that it falsifies a common notion about the earliest dispersals of *H. sapiens* into Europe, which are usually assumed to have occurred during brief climatic ameliorations in Marine Isotope Stage 3 (Hublin 2015). The archaeological and faunal records at Bacho Kiro show that these dHS were already coping with life in colder environments some 44 ka ago (Pederzani et al. 2021; Smith et al. 2020), something that may speak to the adaptability of our species, but which might also reflect the part-Neanderthal biological and cultural heritage of these people.

NEW EVIDENCE FROM WESTERN EUROPE

During the last Ice Age, global sea levels were much lower because of the amount of water stored in enlarged ice caps, and the island of Jersey was connected to France. Excavations between 1911 and 1920 at the site of La Cotte de St Brelade on Jersey found more than 20,000 stone tools from the Middle Paleolithic (an industry associated with the

Neanderthals in Europe), as well as the bones of Ice Age megafauna such as mammoth and woolly rhinoceros (Callow and Cornford 1986). In 1910–1911, thirteen human teeth were also discovered, and because they were large, with robust roots, they were identified as Neanderthal (Keith and Knowles 1912). In the last few years, researchers have re-examined these teeth, with surprising results (Compton et al. 2021). First, from detailed comparisons there were at least two individuals represented, not one as originally assumed. Second, while all the teeth had some Neanderthal traits and their size was consistent with being Neanderthal, several of the teeth lacked features normally found in these ancient humans, while other aspects of their shape looked much more typical of our species, *H. sapiens*. It is known from recent dating work at the site that these teeth are probably less than 48 ka old (Bates et al. 2013), meaning they might represent some of the youngest Neanderthal remains known to date. However, given that it is also known that *H. sapiens* overlapped with Neanderthals in some parts of Europe from more than 40 ka ago and that these populations interbred at times, perhaps the unusual combinations of features in these individuals indicate that the Jersey population had a dual Neanderthal-*sapiens* ancestry in the immediate past (Compton et al. 2021). This is something that could be tested if ancient DNA is preserved in the teeth.

A recent study by Slimak and colleagues (2022) provides further evidence of multiple *H. sapiens* dispersals, with a deciduous upper molar from Layer E at Grotte Mandrin in the Rhône Valley (France) identified morphologically as *H. sapiens* and dated between ~57–51.5 ka. This single tooth was associated with a distinctive stone tool industry called the Neronian, named from the nearby Grotte de Néron, and which is characterized by standardized points interpreted as either very small spear points or possible arrow heads (Slimak 2007). This industry, lying between levels containing Mousterian tools characteristic of Neanderthal occupation and eight additional teeth identified as Neanderthal, is unlike any other in Europe at this time, with the closest parallels found in the Levant and Africa. These discoveries at Grotte Mandrin raise further questions about possible genetic and cultural contacts during this time period, and about possible dispersal routes from western Asia to the Rhône Valley along the northern Mediterranean coast. They also raise questions about the nature and longevity of the Neronian itself, given that this industry has been dated to a much younger age at the related site of Abri du Maras (Ruebens et al. 2022).

This wealth of new data adds to a growing picture of multiple dispersals of early *H. sapiens* into Neanderthal territories in Europe prior to 40 ka, at various times and using different technologies. However, some of these were seemingly brief and transient occupations (for example at Grotte Mandrin), perhaps due to fluctuating environments linked to unstable climates, and rather than envisaging repeated large waves of invaders into Europe, we should perhaps instead imagine small rivulets of people, ebbing and flowing through time. Some of these early range expansions of *H. sapiens* (for example, the populations represented by the Ust'Ishim, Zlatý kůň, and Oase genomes) apparently had no later descendants in Eurasia, indicating that these individuals represent now-vanished lineages of our species (Liu et al. 2021).

WHAT HAPPENED WHEN NEANDERTHALS AND *HOMO SAPIENS* ENCOUNTERED EACH OTHER?

The long debate about whether Neanderthals and *H. sapiens* interbred has finally been resolved by the availability of ancient DNA, and models such as Recent African Origin with Hybridization, and Assimilation (e.g., Bräuer 1984, 1992; Smith 1992; Smith et al. 2017; Trinkaus 2005), now look the most appropriate for the observed data (Galway-Witham and Stringer 2018; Stringer 2014). If gene exchanges between the populations were widespread and the derived traits of *H. sapiens* spread more gradually through demic diffusion, Assimilation will eventually prove the more applicable, whereas evidence that the indigenous populations were predominantly absorbed by dispersing *H. sapiens* in a replacement process would favor Recent African Origin with Hybridization.

There has been a recent and welcome reimagining of the Neanderthals in popular culture and academic writing, emphasizing their humanity and close kinship to us (Gurche et al. 2019; Kubicka et al. 2022; Sykes 2020). However, with an effective evolutionary separation time of perhaps 500 ka between the dHs and dHn lineages, we should be wary of representing these other humans as just a larger-browed version of ourselves. Differences in pelvic and ribcage anatomies suggest clearly distinct physiologies as well as physiques (Churchill 2014; García-Martínez et al. 2020), and there is no precise knowledge of the external appearance of Neanderthals in terms of body, facial, and head hair distribution, and the exact form of elements such as the external ears, eyes, nose, and lips. The brow ridge, ubiquitous in adult Neanderthals, is a much-debated structure (for example, see Russell et al. 1985), but recent research suggests it may have had a signaling function in earlier humans, which could have persisted in Neanderthals (Godinho et al. 2018) and was lost in dHs. This implies that dHs replaced that function with other signals, perhaps in the eyebrows or other facial expressions, or perhaps in a repertoire that involved language or symbolic displays, which might have included cultural adornments such as piercings and tattoos.

When the lineages of *H. sapiens* and *H. neanderthalensis* began to encounter each other some 60 ka ago in Eurasia, there could have been both similarities and differences (most unknowable to us) in appearance, verbal and gestural communication, expression, general behavior, and perhaps even smell, that would have impinged on how they perceived each other at first contact, thus affecting the mechanisms of mate recognition. Would they have seen each other as people, and thus potential allies, mates, or enemies, or even as the next meal? Whatever the answer, it could have varied from one time and place to another, especially given the vagaries of human behaviors. Moreover, as these populations had been diverging from each other for much longer than any of the diverse groups who encountered each other across continents during the so-called 'Age of Discovery,' we might except more profound contrasts in appearance and behavior than were experienced in recent human history. In addition, although the Neanderthals were clearly intelligent and surely had spoken language, language distinctions that developed along the Neanderthal and *H. sapiens* lineages would probably have far exceeded any that exist today. Moreover, there are genetic data suggesting that cognition and vocal tract anatomy were also distinct in *H. sapiens* (Gokhman et al. 2020; Kuhlwilm and Boeckx 2019; Pinson et al. 2022; Weiss et al. 2021), which could have heightened contrasts between the two species of humans.

Whatever the scale of differences between *H. neanderthalensis* and *H. sapiens* at a species level, it is known from a growing body of genetic data that members of their respective populations must have interbred on many occasions, and those matings produced fertile offspring, even though there might have been some level of hybrid infertility in the male line (Kubicka et al. 2022; Mendez et al. 2016; Sankararaman et al. 2016). So, what was the social milieu that led to these sexual encounters? Considering chimpanzees, there are examples of the capture of females from other troops (Wilson and Wrangham 2003), and females of both pre-reproductive and reproductive age have at times been seized from their social groups among recent hunter-gatherer and pastoralist populations (Hrdy 2009). Opportunistic and often covert couplings solicited by individual males or females may take place away from regular partners in gorillas and chimpanzees (Breuer et al. 2016; Roberts and Roberts 2015; Wroblewski et al. 2009), as well as in *H. sapiens.* More structured movements of partners among recent hunter-gatherers vary according to local demographic conditions (Kramer et al. 2017), and thus may also have developed between Neanderthal and *H. sapiens* groups at times.

However, what is intriguing at the moment is that there are several actual or possible examples of interbreeding between late Neanderthal and *H. sapiens* groups that were deciphered from the fossil record and presented here, but all of them so far (apart from the equivocal La Cotte example) are evidenced from *H. sapiens,* not Neanderthal, fossils. Is this because of a sparser genetic record from late Neanderthals (Hajdinjak et al. 2018), or is this an indication that hybrids within Neanderthal social groups were rarer, or were not viable? If a larger sample of genomes from the critical 40–45 ka period maintains the present pattern of Neanderthal DNA entering *H. sapiens* gene pools but not the reverse, then this might provide a mechanism for the demise of Neanderthal populations. If fertile Neanderthals were regularly being absorbed into *H. sapiens* groups (by whatever mechanisms) during that time period, they were effectively also being removed from Neanderthal gene pools, and such a consistent drain of prime-age individuals is not something that could have been sustained for long in small hunter-gatherer groups. Perhaps dispersing *H. sapiens* groups acted like sponges in absorbing pockets of late Neanderthals and maybe that, as much as anything else, led to the eventual demise of the Neanderthals as a viable population.

Recent progress in the recovery of environmental DNA from cave sediments promises to revolutionize our understanding of population relationships on the ground as *H. sapiens* and *H. neanderthalensis* groups interacted with each other. Few European sites in the time period between 40–60 ka contain human fossils, but many more of them could contain traces of human presence in the form of mitochondrial and nuclear genomic material. Research so far demonstrates that sediment DNA can identify humans at the species and individual levels, and this could potentially map the co-existence of different populations, their sex, their kinship relations, and the extent of intermixture between the different populations (Vernot et al. 2021; Zavala et al. 2021). Such breakthroughs could not have been anticipated even a few years ago, and no doubt there will be many more surprises to come. There is still much to learn about the ancient encounters that we have discussed in this paper, which left an indelible genetic mark on humanity today, and which makes their study so intriguing.

ACKNOWLEDGEMENTS

We would like to acknowledge all the authors whose findings are discussed in this paper, and we thank the Calleva Foundation and Human Origins Research Fund for supporting our work. We would also like to thank Marta Mirazón Lahr, David Strait, and a third reviewer for the constructive suggestions that have greatly improved this paper.

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