# Neandertals revised

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**The last decade has seen a significant growth of our knowledge of the Neandertals, a population of Pleistocene hunter-gatherers who lived in (western) Eurasia between ∼400,000 and 40,000 y ago. Starting from a source population deep in the Middle Pleistocene, the hundreds of thousands of years of relative separation between African and Eurasian groups led to the emergence of different phenotypes in Late Pleistocene Europe and Africa. Both recently obtained genetic evidence and archeological data show that the biological and cultural gaps between these populations were probably smaller than previously thought. These data, reviewed here, falsify inferences to the effect that, compared with their near-modern contemporaries in Africa, Neandertals were outliers in terms of behavioral complexity. It is only around 40,000 y ago, tens of thousands of years after anatomically modern humans first left Africa and thousands of years after documented interbreeding between modern humans, Neandertals and Denisovans, that we see major changes in the archeological record, from western Eurasia to Southeast Asia, e.g., the emergence of representational imagery and the colonization of arctic areas and of greater Australia (Sahul).**

Neandertals | early modern humans | Middle Paleolithic | Middle Stone Age

Neandertals were the first extinct hominins identified on the basis of fossil skeletal remains, recovered in 1856 during quarrying work at the Feldhofer Grotte near Düsseldorf, Germany, and baptized as *Homo neanderthalensis* in 1864 (1). Ever since their 19th century discovery, paleoanthropologists and archeologists have been struggling with the interpretation of the skeletal and archeological records of these hominins. Their close relationship to modern humans made Neandertals an interesting "outgroup" for the study of the biological and cultural features characterizing our own species. Hence, for a long time, the field of Neandertal studies has been struggling with a wide variety of viewpoints on Neandertal vs. their modern human contemporaries' behavioral and cognitive differences and similarities and over the role of inferred Neandertal inferiority in their demise, at about 40 ka (1 ka = 1,000 y before present) (2). Recent studies have shed new light on these debates, as a result of new finds and developments in the fields of archeology and paleontology, and by spectacular progress in the study of ancient genomes. Such studies have established that Neandertals did contribute to the modern human gene pool, with all humans who trace their ancestry beyond sub-Saharan Africa carrying Neandertal DNA making up around 1–4% of their genome (3, 4), with the models for estimating this gene flow still developing.

The modern human phenotype evolved in the Middle Pleistocene in Africa and from there expanded its range into Eurasia, reaching the Levant by around 100 ka and possibly surfacing in southern China already at 80 ka (5). In light of admixture between modern humans and a variety of archaic hominins, one can suppose that modern humans were always part of what Pääbo recently called "…a 'hominin metapopulation'-that is, a web of different hominin populations, including Neanderthals, Denisovans and other groups, who were linked by limited, but intermittent or even persistent, gene flow" (6). Interbreeding may have helped migrating modern humans to adapt to non-African environments, profiting from gene variants that had evolved in Neandertals as adaptations to living in the colder settings of Pleistocene midlatitude Eurasia (7), as well as to local pathogens (8, 9). The genetic evidence for (some form of) biological "compatibility" between Neandertals and modern humans has certainly had an impact on the interpretation of the archeological record of Neandertals, by creating "accommodation space" for the view that the purported behavioral "gap" between these two groups in the metapopulation was narrower than most

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[for prominent exceptions, see the work of d'Errico (10) and Zilhão (11)] would have acknowledged less than a decade ago (for a review, see ref. 2). Nevertheless, the view that modern humans were superior in a wide range of domains, including weaponry, subsistence strategies, and cooperation skills, and that this would have led to a fast demise of Neandertals and other archaic populations is still a prominent one (12).

It is these archeological data that will be reviewed in the present paper. We focus on the archeological record created by the Neandertals in the hundreds of thousands of years in which they existed in a wide range of environments over major parts of Eurasia, address the character of their adaptations through their vast geographical range and time span, and compare these with other populations, mostly contemporary near-modern humans in Africa and Asia but also with later modern humans, e.g., those of the Eurasian Upper Paleolithic.

## Neandertals in Time and Space

Whereas a few decades ago, Neandertals were seen as a mainly Late Pleistocene phenomenon, our sister lineage now appears to have a much greater time depth, reaching back far into the Middle Pleistocene. Some of the cranio-mandibular features characteristic for the Late Pleistocene "classic" Neandertals are already present in the Sima de los Huesos (SH) assemblage in Spain at ∼430 ka (13) and are also observable on the Swanscombe (UK) skull of about the same age (14, 15). In congruence with these morphological analyses, recent studies of nuclear DNA sequences retrieved from the SH material also situate that assemblage on the Neandertal evolutionary lineage. This finding implies that the Neandertal-Denisova split must have occurred before ∼430 ka and that ancestors of modern humans split from the source population of Neandertals and Denisovans as early as the beginning of the Middle Pleistocene: 550–765 ka (16).

Good agreement also exists now between studies of morphology and genetics for the very end of the Neandertal lineage. The morphology of the Pestera cu Oase (Romania) fossils, the first modern humans from Europe, dated to 42–39 ka, was (controversially) interpreted as the result of interbreeding between Neandertals and modern humans (17), a view recently confirmed by genetic analysis demonstrating that the inferred hybrid had a Neandertal ancestor four to six generations before his time (18). A study of the modern human genome sequenced from the 45,000-y-old femur from Ust'-Ishim (Siberia) dates Neandertal-modern human interbreeding roughly between 50 and 60 ka (19), in line with the estimates from the Kostenki 14 (Russia) study (20). Interbreeding also occurred much earlier, however, and gene flow went both ways as shown by a genetic contribution from ancient modern humans in Altai Neandertals, the result of interbreeding of the ancestors of these eastern Neandertals with modern humans, an estimated 100,000 y ago (21). These observations indicate that admixture between Neandertals and early modern humans occurred repeatedly in various regions and over several tens of thousands of years.

With earlier claims for a late survival of Neandertals in Europe largely falsified—most proven to be based on radiocarbon samples suffering from incomplete removal of contamination (22–24, but see ref. 25 for some late sites in Iberia)—Neandertal extinction can now be dated to the period 41–39 ka (26). There is significant debate over the age of the earliest modern humans in Europe, but if we limit ourselves to the directly dated human remains, there are no dates before 41.5 ka, the upper range of the Pestera cu Oase material's calibrated C14 age. As one can safely assume that our fossil sample in all likelihood does not sample the very last Neandertal or the very first modern human, an overlap of minimally 2,000 y within Europe can be inferred. However, when discussing the C14 dates for the demise of the Neandertals and the arrival of modern humans, we should keep in mind that we are working in a time period close to the limits of the radiocarbon dating method (27).

The Neandertal fossil record is strongly biased toward Neandertals from Western Europe, an area only about one-fifth the size of their estimated total range but containing about three-quarters of all of the sites which yielded Neandertal remains. This pattern is partly related to the preservation of fossils in caves and rock shelters in the limestone areas of France, Spain, and Italy, and certainly also an artifact of the large amount of fieldwork done in the western tip of Eurasia. In actual fact, the northern, eastern, and southern limits to their distribution are poorly documented, because of striking imbalances in research intensity. Despite occasional claims to the contrary (ref. 28 vs. 29), no unambiguous Neandertal sites are known from areas above 53° north, in western Europe (30), as well as in the eastern parts of their range. As for their southern limits, no skeletal finds are known from Africa, but one can infer the occasional interfingering of the Neandertal range with that of near-modern contemporaries in the Near East. Neandertals were very probably present in the northern parts of the Levant before modern humans were there around 90–100 ka, during Marine Isotope Stage (MIS) 5, with Neandertals again present during MIS 4 (31). The Neandertal sample from the sites of Kebara, Tabun, and Amud (Israel) differs from European contemporaries in craniofacial morphology, to the point that doubts have been expressed about their identification as Neandertals, stressing the morphological variability within both early *sapiens* and Neandertal groups in the region (32).

The eastern part of the Neandertal range overlapped with that of the recently discovered Denisovans (33), thus far mainly known through their genetic signal, as well as through some teeth and postcranial remains from Middle and Late Pleistocene deposits in Denisova Cave in the Altai, a site which also yielded Neandertal remains (34). Neandertals interbred with the Denisovan population, which once must have had a large geographical distribution, from Siberia into tropical Asia. The Denisova site, part of a Neandertal site cluster in southern Siberia (with Okladnikov and Chagyrskaya), is situated in a tributary valley of the Ob drainage system, which 1,500 km to the northwest yielded the Ust'-Ishim fossil, at 57° north, further north than any Neandertal fossil uncovered thus far.

Judging from the distribution of their fossils, Neandertals ranged over an area of ∼10 million km$^2$, i.e., much larger than Australia. Within that area, their presence must have varied significantly, in the rhythms of climatic variations so characteristic for Pleistocene midlatitude environments: some areas may have seen a semicontinuous presence of groups of Neandertals, whereas in other parts of their range, discontinuity may have been more common. The strong bias in the distribution of Neandertal fossils, the poor state of sampling of major parts of Asia, and the results of genetic studies (35) force us to be careful in making inferences on the core and peripheries of the Neandertal world. What is clear is that Neandertal populations in the west differed from the ones in the east (21, 35) and that they were very dynamic on both regional and larger geographical scales. High-resolution data from northwestern Europe for instance show clear phases of presence and absence of Neandertals in the Late Pleistocene (36, 37), very probably the result of a process of repeated phases of colonization, regional extinction, and recolonization, also during earlier glacial–interglacial cycles (37). This process must have been an important factor in the demography of these populations, including their limited genetic variation (15, 38): genetic studies show that (late) Neandertal populations had small effective population sizes and were inbred, not only in relation to extant humans within Europe, but also in comparison with their Denisovan contemporaries (34): they were "thin on the ground" (39) indeed, even though making quantitative assessments of population densities in any given area is problematic (40).

## Neandertal Ways of Life

Neandertals were large-brained and large-bodied robust hominins, their long and flat skulls characterized by features that distinguish them from other members of the genus *Homo*, including a strong midfacial prognathism and a globular shape of the cranium when viewed from behind. Their overall body form was characterized by a short stature, a wide trunk, and a "barrel-shaped" chest, somewhat comparable to today's humans from colder regions (39), and possibly entailing higher energetic needs compared with modern humans (41).

Considerable attention has been given to the question whether they showed the prolonged growth period of modern humans, an important characteristic of the knowledge-intensive hunter-gatherer niche (42). Focusing on tooth growth as an indication for somatic growth, one study concluded that Neandertal dental growth patterns are encompassed within the modern human range of interpopulation variation (43). More recent studies found evidence for faster dental maturation in most Neandertals (44), inferred to be consistent with cranial evidence for subtle developmental differences between Neanderthals and *Homo sapiens* (45, 46), which could have impacted the length of the critical learning period. Analysis of an immature hominin mandible from the more than 800,000-y-old TD6 level at Atapuerca (Spain), however, suggests that the source population of both Neandertals and modern humans already had a fully modern pattern of dental development (47).

A series of comparative studies of young vs. older adult mortality distributions for Neandertals and early modern humans, as well as early Upper Paleolithic, addressed possible differences between the populations (48, 49). These studies indicate "...only subtle and paleontologically invisible changes in human paleodemographics with the establishment of modern humans " (49), an assessment that might need to be qualified in the light of the difficulties in establishing longevity, because of the problems with aging adult skulls. Interestingly, the traumas identified in Neandertal skeletal remains are no different from extant hunter-gatherers (50, 51).

Hunting clearly was the main method of meat procurement by Neandertals (52, 53), from the very beginning of the lineage onward, as illustrated by the ~300,000-y-old carefully crafted (54) wooden spears and the associated remains of large ungulate prey animals at Schőningen (Germany) (55–57). Stone-tipped spears seem to have been part of their hunting equipment too (58–61). They hunted a wide range of animals including reindeer and horse in colder settings up to the larger herbivores of interglacial forested environments, such as rhinoceros (62), deer, and bovids (63), with some assemblages documenting a strong focus on prey animals in their prime and patterns of faunal exploitation comparable to recent hunter-gatherers (64). Earlier carbon and nitrogen isotope studies of collagen from Neandertal skeletal remains suggested that they were top-level carnivores obtaining most of their proteins from terrestrial animals, likely medium and large herbivores such as bovids and horses (65), but the Neandertals sampled were mostly from northern open and cold stage environmental settings. These results have been complemented by studies demonstrating a much broader diet, including aquatic foods (fish and molluscs), small animals (including tortoises, birds, and rabbits), and a variety of plant resources across their range (2, 66, 67). Some of those plant remains were very probably cooked, as suggested by plant microfossils recovered from the calculus of Neandertal teeth (68), a new source of data regarding the food of early hominins (69–71). A recent study (67) compared Neandertal plant use to that of African Middle Stone Age (MSA) populations and Upper Paleolithic groups, but failed to find any differences between Neandertals and contemporary near-modern humans, as well as more recent ones.

Marine shellfish collecting, seen by some as a distinctive trait of modern humans (72), has been documented at various Neandertal sites on the Iberian peninsula. Bajondillo Cave (Spain), close to the sea shore during all phases of the Pleistocene, yielded evidence for continuous use of coastal resources between ~150 and 40 ka (73), its early dates coinciding with the first evidence for exploitation of marine resources by early modern humans at Pinnacle Point in South Africa. As discussed by Klein and Bird (74), near-coastal rockshelters with fills that formed during low sea level periods are very rare, limited to coasts with a steep offshore profile, such as at Bajondilla Cave. The known record thus cannot show when people, Neandertals or archaic humans, first collected shellfish. Given the high nutritional value and the ease with which shellfish can be collected, this very probably started long before 150,000 y ago (75).

With the beginning of the Neandertal lineage now situated in the first half of the Middle Pleistocene, the stone tools produced by the earliest Neandertals can be classified as Acheulean, a handaxe-dominated technological tradition that ended approximately 300,000 y ago in Europe. The Acheulean saw a distribution over major parts of the Old World, including Africa, Europe, and parts of Asia. The beginning of the Middle Paleolithic, around MIS 8, is characterized by the Levallois method, a technique to extract blanks of predetermined form from carefully prepared cores. From around 300 ka onward, Neandertals again shared with their MSA contemporaries the use of this Levallois method (76), whereas alongside the Levallois technique, older, more expedient, techniques kept on being used by Middle and Late Pleistocene African and Eurasian populations. The blanks obtained by the Levallois and other techniques could be used as such or after having been retouched for sharpness or strength. The Middle Paleolithic is a period of technological diversity, with the production of flakes, blades, points, and to a lesser extent, bifacial pieces, documented throughout the entire ~250,000 y (37) in both the Neandertal record and in the record of near-modern humans in the Levant (77). The higher resolution of data for the later (i.e., Late Pleistocene) parts of the Middle Paleolithic has enabled the identification of clear spatiotemporal units, including the Mousterian of Acheulian Tradition (MTA) of Southwest France (78) and the Quina Mousterian, dated between 70 and 40 ka. The Dordogne area in southwest France is famous for a recurrent succession of Ferrassie, Quina, and MTA (79, 80), whereas in Spain, Quina can be found directly underneath transitional or Upper Paleolithic assemblages (81). The Keilmessergruppen (KMG) of Central Europe, dated between MIS 5 and MIS 3, have bifacial tools that are technologically and typologically well-defined guide fossils. The KMG can be further subdivided into separate inventory types in a clear chronological succession and with regional differentiation (82, 83). As detailed elsewhere (2), these technocomplexes may in terms of their duration have been similar to the contemporaneous South African MSA technocomplexes of the Stillbay and the Howiesons Poort.

Neandertal lithic assemblages show a strong focus on the exploitation of local (<5 km from the site) raw materials, with transport of stone artifacts over larger distances (>50 km) occurring in small, variable proportions. One of the striking features of the Middle Paleolithic record is the ubiquitous transport of stone artifacts of a wide variety of forms, selected by Neandertals using criteria that were sometimes far removed from what archeologists consider to be desired end products of knapping activities, including small irregular flakes and, in a few cases, even chunks, accidental byproducts of flaking (84). Some rock shelter sites show the reuse of already patinated blanks or the introduction of naturally broken pieces of flint, geofacts picked up en route and used as blanks for tool production. This relaxed attitude toward tool blanks is comparable to what has been documented in the Australian record (85), whereas also earlier phases of the Upper Paleolithic—including the Aurignacian—show strong similarities to Middle Paleolithic raw material strategies, at least in the well-studied Aquitaine basin in southwestern France (84).

The mobile character of Neandertal lifestyles, as suggested by the spatial fragmentation of their stone tool production, is also borne out by their archeological sites, where only very little investment in site furniture (86), i.e., archeologically visible remains of dwelling structures or stone-lined fire-places, has been documented, as is the case for their African MSA contemporaries also. If Neandertals built structures (87), they were generally not significant enough to leave clear archeological traces.

There exists considerable debate over the antiquity of fire use in the human lineage, but both the European (88) and Levantine record (89) suggest that fire became a fixed part of the hominin repertoire around 350,000 y ago—even though some have suggested that Neandertals, although proficient fire users, were not able to produce fire at will (90, 91). Most Neandertal sites yielded traces of fire use, at some sites in the form of stacked fireplaces—simple lenses of ash and charcoal—testifying to repetitive occurrences of fires over longer periods of time, as at Roc de Marsal (France) and Kebara (Israel), features comparable to the fire places of the Klasies River Mouth caves in South Africa (92).

The heat treatment of silcrete in the African MSA has been presented as "the earliest known pyrotechnology" (12), dating back to ∼160 ka (93). The complexity of heat treatment (i.e., requiring more or less steps for its realization) is debated (12, 94, 95), with a recent study yielding strong evidence that it could be conducted directly using an open fire, alongside other daily, fire-related activities (96). It certainly is a simple procedure compared with the complex technology recipe for Neandertal glues, based on using fire to synthesize pitch from birch bark, through a multistep process that relied on strict control of temperature and required a dry distillation excluding oxygen (88, 97). The oldest finds date to more than 200 ka (98), and other such pitches come from Late Pleistocene Neandertal sites in Germany of approximately 80 ka (99). Like modern humans heating their silcrete at Pinnacle Point, Neandertals also used fire as a transformative technology to heat treat existing natural materials, such as bitumen for hafting purposes (100).

Late Pleistocene near-modern humans in South Africa are often credited with a "complex cognition" that would have produced a "symbolically mediated worldview and facilitated language ability" (12). The use of iron oxides (purportedly as pigments for personal decoration), the use of transported marine shells, and the presence of cross-hatched lines on pieces of bone and ochre are often taken as a proxy for such complex cognition. However, translating archeological finds into statements about complex cognition and use of symbols involves a series of inferential steps, only some of which can be supported by solid evidence, given the elusive character of symbols from past societies (101). Comparable chains of inference have been built around evidence for Neandertal use of manganese blocs (102), transported and ochre-smeared marine shells (103, 104), use of raptor claws (105, 106), and Neandertal exploitation of bird feathers (105, 107). Such uses have been documented repeatedly, at various sites, and hence seem to have been part of the Neandertal behavioral repertoire. The context of the use (functional, symbolical, both) of these finds is unknown, as explicitly stated for the early (250 ka) ochre finds at Maastricht-Belvédère (The Netherlands) (108), and needs further exploration, as underlined by a recent study of manganese dioxides in late Middle Paleolithic sites in southwest France (109). What is important here is that we have comparable evidence both from the Neandertal world, as well as from the African MSA. It should not come as a surprise that the record from these two areas indicates somewhat different trajectories, with, for example, the use of manganese very rare in the MSA but common in the later Middle Paleolithic, and the late Neandertals (of the so-called Châtelperronian) developing their own ways of producing personal ornaments (110).

A geometric engraving earlier than the ones from Blombos in South Africa has recently been published from the *Homo erectus* site of Trinil, Java. The marking, dated to around 450 ka (75), is a unique case thus far, but it shows that such engravings were within the range of the capacities of the hominin metapopulation already in the middle part of the Middle Pleistocene.

A lot of ink has been spilled on another issue thought to be relevant for the symbolic domains of the Neandertal world: burials. The presence of a number of fully articulated Neandertal skeletons (see ref. 111, table S7 for a west European sample) suggests that some Neandertals covered dead conspecifics with sediments, i.e., that they buried their dead. However, as ref. 112 emphasizes, we have to differentiate between a burial—a body covered with sediment—and a funeral, which denotes a symbolic ritual possibly based on spiritual beliefs. In the absence of unambiguous grave goods associated with Neandertal skeletons, we have no evidence whatsoever for funerals in the Neandertal record. Burials by contemporary near-modern humans are limited to the ones from Qafzeh and Skuhl in Israel, strongly resembling those of the Neandertals ". . . in their essential simplicity" (92). This description applies to many Upper Paleolithic burials also, however: a recent review of the Upper Paleolithic burials in Eurasia (113) concludes (*i*) that for the whole of the Eurasian Upper Paleolithic, there is only a small number of burials (3/1,000 y), (*ii*) the earliest Upper Paleolithic burials postdate the arrival of modern humans in Europe by ∼10,000 y, (*iii*) Upper Paleolithic burials differ widely in terms of elaborateness, and (*iv*) in many cases, the evidence for funerary rituals is very thin, with the authors suggesting that most of the items traditionally considered as Upper Paleolithic grave goods are probably personal ornaments worn in life. Elaborate forms of burial behavior certainly existed within the Upper Paleolithic (see ref. 114 for an overview), as exemplified by the 27,000-y-old ochre-covered infant burials of Krems-Wachtberg (Austria) (115) and the 2,000-y younger Sunghir (Russia) burials, but most burials were vastly more sober and not as different from the Neandertal record as commonly thought.

## Discussion

Given the hundreds of thousands of years of (relatively) separate evolution, the huge geographical areas at stake (Africa, western Eurasia), and the small sample sizes at our disposal, it would be too far-fetched to state that Neandertals and their MSA contemporaries were indistinguishable in their archeology. As mentioned above, for instance, in the later phases of the MSA, as well as of the Middle Paleolitic, different technological trajectories developed, and on entering western Eurasia, some modern humans seem to have ventured further north than any of the preceding or contemporary Neandertals. However, it is also a fact that the archeological records of Neandertals and their African near-modern human contemporaries are very similar in terms of what were once thought to be standard markers of modern cognitive and behavioral capacities, such as diversity of subsistence strategies and diet, use of minerals, use and transport of lithics, shells, personal ornaments, and hafting, and pyrotechnology. As discussed elsewhere (2), these findings are at odds with the view that extinction and replacement of Neandertals should be explained mainly in terms of substantial cognitive and technological differences with their African contemporaries (12). Rather, the Neandertal demise appears to have resulted from a complex and protracted process including multiple factors such as low Neandertal population density, interbreeding with some cultural contact, possible male hybrid sterility, and contraction in geographic distribution, followed by genetic swamping and assimilation by modern human immigrants. There is no doubt that the Neandertal phenotype ultimately disappeared through (some form of) competition with modern humans who outbred the Neandertals, even though the specifics of that process still are largely unexplored. That process must have varied regionally, with in some regions, members of what we tend to call the two populations actually interacting, whereas in others, e.g., the Swabian Jura (Germany) (116), immigrants may have entered territory that had not seen a Neandertal presence for some time. With as a caveat the absence of any archeology unambiguously relatable to the Denisovan part of the Middle and Late Pleistocene hominin "metapopulation," it is fair to say that a major change in the archeological record occurs only around 40 ka, with the first and repetitive production of 3D sculptures (117), the almost simultaneous emergence of rock art in the form of hand stencils (118), and figurative paintings of animals, both in western Europe and more than 10,000 km to the east, at Sulawesi (119, 120). We have to bear in mind here that the ages for the oldest rock art from Europe and from Asia are minimum dates, obtained on overlying (dated) calcite accretions, and that the art itself may prove to be older. However, from the hundreds of thousands of years in which Neandertals and their African near-modern contemporaries littered their landscapes with all kinds of artifacts, nothing has been retrieved that is in any way comparable to the visual representations ("art") and the general increase in diversity in material culture we see from around 40 ka onward. These developments coincided with a significant range expansion of modern humans, for the first time in human history colonizing the arctic parts of the Old World (121, 122), as well as moving into Sahul (123), crossing a major biogeographical boundary that had prevented hominin eastward migration for more than a million years.

There exists a range of explanations for these major changes within the record of modern humans, including demographic factors, e.g., changes in the population size of modern humans (see ref. 124 for a review) and a key neural mutation thought to have promoted the final development of the modern human brain (125). It has also been suggested that the new types of material culture considered typical for the Upper Paleolithic cultures, evolved among populations of modern humans only as they made "...ever further inroads into the range of archaic hominins," and that it may have been these "frontier settings" in which modern symbolic behavior emerged (126). At the same time, it is also worth stressing that not all modern humans from 40 ka onward produced a record comparable to that of the European Upper Paleolithic, as famously shown by the record from Pleistocene greater Australia (123, 127).

One of the questions in the relationship between Neandertals and modern humans is how to explain how the Neandertal phenotype, adapted over a period of more than 300,000 y to the predominantly colder conditions in (western) Eurasia, came to be replaced within a few thousand years by a modern human phenotype, largely developed in the tropical and subtropical settings of (sub)Saharan Africa. The presence of near modern humans in the Levant at around 100 ka, however, already qualified any view of an immediate replacement of Neandertals by migrating modern humans as soon as they left Africa. The recent study of modern human teeth from southern China, if substantiated by future research, would be of relevance here too, as the authors claim that modern humans were already present in eastern Asia minimally 40,000 y before they showed up in Europe, suggesting that Neandertals could indeed have been a long-time barrier for modern human expansion into western Eurasia (5).

## Conclusion

As far as the archeological record goes, the cultural capacities of the late Middle and early Late Pleistocene populations in Africa and Eurasia were remarkably comparable, with purported cultural markers such as exploitation of coastal resources and complex recipe technologies present in both the modern human MSA and the Neandertal record (the Neandertal pitches being our best and earliest example of a complex recipe technology). It is only around 40 ka, tens of thousands of years after the modern human phenotype appeared outside of Africa, and thousands of years after the first interbreeding between modern humans, Neandertals, and Denisovans occurred, that we see a major change in the archeological record, on both sides of the spatial distribution of modern humans, in western Eurasia and in Southeast Asia, reflected in the production of 2D and 3D visual representations and in a significant range expansion of modern humans. Explaining this transformation in terms of models that acknowledge the Neandertal archeological record and the biological and cultural fluidity within the hominin metapopulation is the challenge for the next decade.

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