

Human Origins and Language Origins 1: A Polycentric Scenario for Biocultural Niche Expansion

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ABSTRACT

This article presents a gradualist perspective on material and symbolic niche construction and expansion that integrates data and theories from archaeology, biology, genetics, linguistics, neuroscience, psychology, and semiotics. Empirical evidence is reviewed from the broader archaeological inventory of material culture (lithics and bone artifacts, pigments, ornaments, other material signs) and from evidence for ecological niche expansion. The evidence supports an account centred on the polycentric and asynchronous emergence of symbolic practices across diverse human populations. The complex, multi-regional nature of human origins and language origins highlights the dynamic interplay between biological and cultural evolution. We reject monocausal explanations implicating a unique speciation event for symbolization and language and any theorization of language as an “add-on” in human evolution, stressing rather how the cognitive foundations of complex technical practices and symbolic practices co-evolved with the evolution of the human developmental niche. Our findings necessitate a re-evaluation of traditional theories of language origin and cognitive evolution, proposing a more integrative and nuanced understanding of the human evolutionary trajectory, situated in an *EvoDevoSocio* perspective on human biocultural evolution.

1. INTRODUCTION

Human origins and language origins (hereafter HOLO when referring to this article and that of Arbib et al. 2027 [this issue]), are distinct but related interdisciplinary fields, which despite their evident mutual relevance have yet to be fully integrated.¹ Half a century ago, the questions “how, when and where did language originate” were virtually absent from debate in the sciences of language, evolution, and human (pre-)history. If they were addressed, this was mainly in the context of ontogenetic language development (Lock 1978) and studies of ape language learning and teaching (Gardner and Gardner 1969). The field of language origins and evolution began its revival in the late 1980s (Lock and Peters 1996), acquiring added impetus by developments around the turn of the century in archaeology (Blench and Spriggs 1998; d’Errico et al. 2003) and comparative animal behavior (Oller and Griebel 2004; Whiten et al. 1999; 2001). It has since become a major, and contested, transdisciplinary research area. Much controversy has focused on a trio of questions. First, did language (i) emerge abruptly and autonomously or (ii) evolve gradually from nonlinguistic forms of communication and cognition? Second, is the defining feature of language (i) recursive syntax or (ii) other attributes, such as displacement (Corballis 2018; Hockett 1960) or normativity (Itkonen 1983), either alone or in combination? Third, is language (i) a relatively recent human faculty, appearing with or after the emergence of *Homo sapiens* or (ii) a capacity that evolved gradually over the course of hominin prehistory? We can label the first answer to each of these questions as, respectively, *autonomy*, *recursion* and *recency*. One hypothesis, associated with generative linguistics, favors option (i) for all three issues (Berwick and Chomsky 2016). Alternatives range from favoring (ii) in all cases (Dediu and Levinson 2018, 2013), to rejecting autonomy and recency but (largely) favoring recursion (Corballis 2017), to rejecting autonomy but accepting recursion and (probably) recency (Arbib 2012).

These issues bring others in their train, such as the relationship between language and human and non-human nonverbal communication, such as alarm calls, gestures and pantomime; the relationships between linguistic complexity, social complexity, and the complexity of other cognitive capacities, practical skills and behavioral repertoires, the evolution of the human brain, and the genetic history of the hominin line. Here (HOLO 1) and in HOLO 2 (Arbib et al. 2027 [this issue]), we offer an integrative approach to human origins, language origins and language evolution through the emergence of Evolutionarily Modern Languages (EMLs), in which we address all these dimensions. Rejecting accounts that identify the emergence of language with unique speciation events or sudden genetic mutations (e.g., Bolhuis et al. 2014; Chomsky 1986, 1988; Everaert et al. 2017; Klein 2000, 2009; Maricic et al. 2012; Tattersall 2017; Wynn and Coolidge 2011), we propose a gradualist, biocultural approach that situates changes in the human organism in relation to changes in the material, symbolic, and communicative niches constructed by and sustaining human societies.

The present paper foregrounds the hominin archaeological record in material and symbolic culture. Our account integrates theory, data, and associated timelines from archaeology, developmental and evolutionary biology, genetics, linguistics, neuroscience, paleoanthropology, psychology, and semiotics. Section 2 articulates our overall theoretical framework, providing an ecological, developmental, and evolutionary context against which data from archaeology, paleoanthropology, and comparative behavioral science will be evaluated. This overall theoretical framework can be encapsulated in two inter-related “tag-lines,” *biocultural niche construction* and *EvoDevoSocio co-evolution*. We link the evolutionary process of human *niche expansion* with augmented *epigenetic development*. As well as defining this terminology, we introduce and define two further theoretical notions, *semiosphere* and *technosphere*.

Section 3, “Pathways to ‘modern’ human biocultural niches,” reviews and synthesizes archaeological, genetic, geological, and paleoanthropological evidence, building an account in which late human evolution is conceived in terms of genetic and cultural hybridization giving rise to biocultural niche diversification and expansion. This is the fundamental matrix within which the invention and use of symbolic artifacts and communicative vehicles accelerated, ultimately giving rise to Evolutionarily Modern Languages.

In Section 4, “Materiality and Meaning-Making,” we integrate a minimal conceptual clarification of symbolic representation with a critical examination of the archaeological record of material signs. We outline working definitions of symbol and symbolization sufficient for grounding archaeological inference, emphasizing communicative representation as a socially conventionalized relationship between sign-users. On this basis, we review evidence for pigments, body ornamentation, mortuary and funerary practices, abstract engravings, drawings and paintings, and figurative representations, and evaluate alternative interpretations of these artifacts and the practices required for their production in relation to their implications for symbolization and language. We suggest that, although niche expansion carries a tendency toward fragmentation, this was counteracted by cultural borrowing and hybridization, leading to a progressive complexification of the semiosphere and the emergence of a shared social imaginary (Castoriadis 1987), in which the actual and the fictive blend and interact, expressed in languages, images, and symbolic artifacts.

Section 5, “Looking ahead,” briefly summarizes our proposals, concluding with a signposting of the topics that are focused in HOLO 2 (Arbib et al. 2027 [this issue]). The arguments and evidence we present compel a re-evaluation of theories of human origins and language origins and their evolution, strongly suggesting a *polycentric* emergence and evolution of human niches, including the niche of symbolic practices.

New evidence about the human past appears at an accelerating rate, and our account is (and should be) vulnerable to empirical disconfirmation. New synthetic accounts of

language evolution are also appearing. In the landscape of contemporary cognitive science, our approach may reasonably be situated within the general perspective of “4E” (embodied, embedded, extended, enactive) (Newen et al. 2018) or “grounded” (Dove 2022) approaches. Most 4E/Grounded approaches, however, neglect two equally important E’s—ecological and epigenetic—and do not address in any depth the evolution of language and symbolic cognition. Two recent books (Planer and Sterelny 2021; Watkins 2024) have adopted theoretical stances that overlap with those advanced here. We share with the first of these an emphasis on gradual complexification of lifeways/biocultural niches and symbolic practices (see also Hovers and Belfer-Cohen 2024), but differ on the key issue of understanding symbolization and language in the context of animal signals. We share with the second an appeal to epigenetics, and the importance of imaginative world-building. We cannot engage in an in-depth dialogue with these or other recent works, fruitful as such a dialogue might be, but it is encouraging that the outlines of a unified new paradigm are clearly discernible. We are confident that the overall framework we present here is plausible, convincing, and capable of serving as a platform for further research and development.

2. EVODEVOSOCIO: EVOLVING, EXPANDING HUMAN BIOCULTURAL NICHES

2.1. NICHE CONSTRUCTION, CULTURE, AND INHERITANCE

From evolutionary biology, we draw upon the interfacing of evolution with ecology in *niche construction theory* (NCT), which we integrate with the concept from developmental biology of *epigenesis*. NCT highlights the ways in which species behaviorally modify their own and each other’s environmental niches—think, for example, of the dams constructed by beavers. Such constructive modifications in turn modify the selective pressures governing their own evolution and that of other species. Laland et al. (2000: 134) note that niche construction may involve “organisms choosing or changing their habitats, or ... constructing artefacts leading to an evolutionary response.” Both of these, in the form of successive waves of migration to increasingly diverse habitats and the accumulating and increasingly diverse inventories of artifacts, with their associated repertoires of knowledge and skills, are evidenced in the human archaeological record. It is this interweaving of geographical dispersal and artifactual and symbolic complexification that we refer to as *human niche expansion*. It was in this context that the symbolic artifact/niche that we call *language* originated. Conceptualizing language as a quasi-artifactual biocultural niche is directly at odds, as is our account in general, with nativist and modularist theories (Pinker 1995). It also differs from, and extends, NCT-based accounts that have proposed that hominin niche construction created conditions favorable for the emergence and evolution of language (Odling-Smee and Laland 2009), by adopting a thoroughgoing externalist, social, normative theory of language (Sinha 2009, 2025).

In NCT, constructed niches are not just contexts for selection, but an integral part of what is selected and inherited: “[W]hat is really replicated is a *biocultural complex*, with a composite array of information (acquired through multiple processes and stored at different levels) and inherited resources” [our italics] (Laland et al. 2000: 144). Any biocultural complex can be thought of as comprising a network of overlapping and nested niches, some of which are artifactual and some of which (including the proximate biome) are “given” by the natural environment. The socio-cultural dimension of the human biocultural niche complex encompasses material and symbolic artifacts supporting and embodying practices, values, and cognitive systems. It includes languages, technologies, ideologies, moral systems, and religions, and has been analysed in terms of constructs such as *habitus* (Bourdieu 1977), social schema (Arbib and Hesse 1986), and cultural model (Shore 1996). Cultural evolution (especially in the time frame leading to and succeeding the emergence of EMLs) has become ever more autonomous (though never detached) from changes in the human genome, leading to accelerating, cumulative changes and increasing diversity in human biocultural niches.

Of fundamental importance for the evolution of the human biocultural complex, the modern human organism and the individual human being is the *developmental niche* (Sterelny 2011; Super and Harkness 1986). Infancy, childhood and adolescence are not only biological stages of organismic development, but also developmental stages of an “extended ontogenetic system” (Packer and Cole 2019) that develops along with the maturational processes underlying the individual’s development. This developmental and developing niche includes as its most important component other human beings, including the caregiving adults and older children who participate in the co-construction of its material, communicative, and symbolic properties. Trappes (2021: 23) points out that, although NCT is motivated by and argued for as a unification of evolutionary and ecological perspectives, the concept of niche employed in NCT is defined in terms of selection pressures, whereas the ecological niche can be more loosely defined as “the factors in the environment that allow a species to persist.” The inclusion of the niche of development as key to the evolution of the human biocultural complex can be seen as a further step to bridging the residual evolution-ecology gap in NCT.

The communicative dimension of the human biocultural niche gained in importance as ontogenetic human development came increasingly to necessitate guided learning of socially conventional patterns of praxis and communication (Wood et al. 1976). As Arbib (2012: 166) observes, “the prolonged period of infant dependency ... combines with the willingness of adults to act as caregivers and the consequent development of social structures to provide the conditions for complex social learning.” The self-constructed symbolic artifactual niche of language—what the semiotician Lotman (1990) called the *semiosphere*—and the niche sub-complex of material artifacts enabling and resulting from constructive praxis (what we call, by analogy, the

technosphere) co-evolved in concert with the developmental niche of infancy and childhood, providing a selective environment for the evolution of human ontogenesis (Sinha 2015) and of teaching and learning, a topic we address in HOLO 2 (Arbib et al. 2027 [this issue]). What, then, was the mechanism underpinning this biocultural co-evolutionary process?

2.2. EPIGENESIS

Odling-Smee et al. (2003: 366) emphasize that NCT “re-establishes the organism [rather than the gene—authors’ note] as the central unit of human evolution, not as vehicle but as replicator.” The same emphasis on organism-level change and development is at the heart of a key concept from developmental biology: *epigenesis*. Epigenesis and epigenetics are terms referring to inheritance processes and mechanisms, at different levels ranging from the molecular (Allis and Jenuwein 2016) to the organismic, that are controlled or modulated by factors additional to those inscribed in the genome (Ashe et al. 2021). C.H. Waddington (1957) conveyed the central insight of the epigenetic approach to embryogenesis and ontogenesis in terms of the visual metaphor of the *epigenetic landscape* (Figure 1). Alternative stable developmental trajectories are represented by the “valleys” that canalize development to a finite set of end-states despite minor disturbances. Following more significant and disruptive genetic or environmental changes, the topography can be modified, leading to novel end-states.

Epigenetic development is characteristic, as the genetic epistemologist Jean Piaget (1979) recognized, of behavioral and cognitive, as well as morphological, ontogenetic development. Epigenetic theories receive support from neural imaging studies showing the effects of cultural evolution on developing neural connections. For example, Dehaene et al. (2010) have shown that learning to read changes the cortical networks for vision and language, and such results have led Dehaene and Cohen (2007) to hypothesize that culture may “recycle” cortical maps to serve purposes that played no role in the biological evolution that produced them.² Colagè and d’Errico (2020) and d’Errico and Colagè (2023) have argued that such cases exemplify a more general mechanism whereby population-level cultural innovation impacts neural substrates at the level of individual organism via “cultural neural reuse.” Epigenetic processes are therefore central to understanding the relationship between social and cultural change, individual adaptive learning, and the evolution of cognition.

The relationship between developmental and evolutionary theory was further elaborated by Jablonka and Lamb (1995) in their Evolutionary-Developmental (*Evo-Devo*) approach, exploring dynamically inter-related ontogenetic and phylogenetic processes in human evolution (Hall 2012). Jablonka and Lamb emphasize that phenotypic selection must operate on genes that mediate development as well as those related to the functioning of the developed organism. The organism’s genotype provides a platform of sequentially emerging and unfolding initial states whose

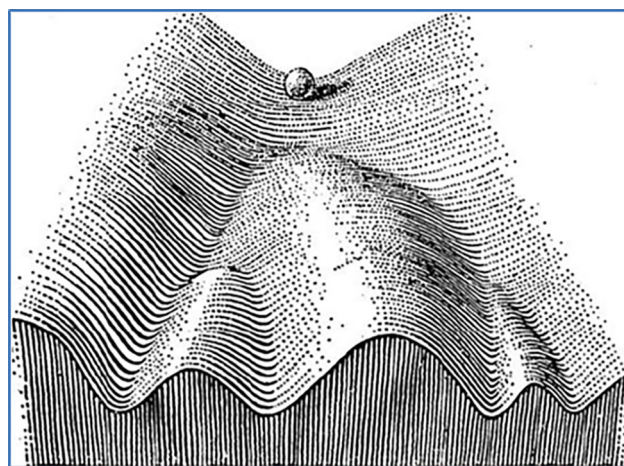


Figure 1. Part of an Epigenetic Landscape. “The path followed by the ball, as it rolls down towards the spectator, corresponds to the developmental history of a particular part of the egg. There is first an alternative, towards the right or the left. Along the former path, a second alternative is offered; along the path to the left, the main channel continues leftwards, but there is an alternative path which, however, can only be reached over a threshold.” (re-produced from Waddington [1957: 29: Figure 4]).

relatively invariant timing and ordering is governed by *regulatory genes* controlling the developmental expression of specific subsets of the genome. Because regulatory genes, like any other genes, may be subject to selection pressures, *epigenesis is a developmental process that has itself evolved*. To put it simply, the developmental trajectories of more complex organisms and more complex behaviors are subject to greater degrees of mediation by regulatory genes than simpler ones, whose genetic expression is relatively more determinate. Or, even more simply, innate behaviors are characteristically found at earlier developmental and evolutionary stages, while epigenetic plasticity is augmented in the development and evolution of more complex behavior.

Social learning of complex skill repertoires, including language, is optimized by the extended childhood of the current members of our species and our close relatives, including Neanderthals (Ponce de León et al. 2016), when compared with extant non-human primate species (Gopnik 2020). There is evidence, however, that anatomically modern humans have an extended period of infancy and childhood even compared with Neanderthals (Smith 2013); Been et al. (2026) also present evidence of accelerated early somatic and endocranial growth in Neanderthal as compared to *H. sapiens* infants. The augmentation of epigenesis, and its associated extended period of developmental plasticity, is evolutionarily advantageous for developing humans, whose multiple organism-niche couplings permit and accelerate social learning in diverse biocultural niche complexes (Sinha 2025). In turn, “the ability to regulate aspects of development in response to environmental cues, is hypothesized to evolve in response to environmental hetero-

geneity and may facilitate dispersal, novel habitat occupation, and niche construction” (McPherson 2025).

Augmented developmental plasticity, and the evolution of an extended life course, are thus integrally connected with human niche expansion, in a dynamic of reciprocal causation and influence. The uniquely developed epigenetic plasticity of human development is the biological foundation, then, both of the evolution of the human life course (Sinha 2015; Suman 2024), and of the “adaptation to adaptation” that is the signature of our species. Since the human developmental niche is subject to change both in ontogenesis and phylogenesis, it is, strictly speaking, the developing *phenogenotypic organism/niche* (Laland et al. 2000) that integrates the other components of the human biocultural niche complex. The integration of niche construction and epigenetic approaches, in the context of social processes occurring at different levels of granularity, is foundational to the *EvoDevoSocio* approach (Arbib 2018) adopted here, in which ontogenesis is both a key adaptive site and the evolutionary mediator of the co-evolution of the component niches of the human biocultural niche complex. We thus envisage human biocultural evolution as a progressive increase in the systemic complexity of multiple, dynamically inter-related structural couplings (Capra 2022; Maturana and Varela 1987) between niches, mediated by and co-evolving with the developing human organism, in increasingly diverse niche complexes. In Section 3 we examine how these processes are reflected in the archaeological and paleoanthropological record.

3. PATHWAYS TO “MODERN” HUMAN BIOCULTURAL NICHES

The terms “modern” and “modernity” recur throughout the archaeological and evolutionary literature. Much of this usage is, however, problematic (Majkić 2024) since the assumption that anatomical, behavioral, cognitive, cultural, and linguistic “modernities” arrived together as a single package is not supported by current evidence. Absence of evidence is not evidence of absence, but it is striking that neither innovation in technology, nor the emergence of the first manifestations of human material artifactual signs, can be isomorphically mapped to speciation events (Colagè and d’Errico 2020) or to evolutionary changes in the human genome. In fact, variation between different domains in which evolutionary processes play out is apparent as far back as we might wish to go in the hominization process. In this section we review archaeological data consistent with a complex demographic, genetic, and cultural scenario for “modern” human origins, setting the scene for a biocultural account situating the emergence and evolution of language in successive, *polycentric niche expansions* of diverse populations within the genus *Homo*. This scenario entails a gradual, asynchronous biological and cultural evolution in different parts of Africa and Eurasia, leading to anatomical modernity in Africa, not before c. 100 Ka.

3.1. HUMAN ANCESTRY

Around 6–7 Ma (million years ago), the hominin line (ex-

emplified by species like *Sahelanthropus tchadensis*) diverged from the Latest Common Ancestor with great apes (*LCA-ga*). The former species is characterized by a combination of primitive and derived traits, such as a small brain size similar to apes and a flatter face more typical of later hominins, suggesting it may have been a bipedal walker. However, its taxonomic classification remains uncertain due to the limited fossil evidence and debates over whether its characteristics are closer to those of hominins or non-hominin ancestors (Macchiarelli et al. 2020). *Australopithecus* species emerged around 4 to 2 Ma, with *Australopithecus afarensis* being one of the most well known representatives. These species demonstrated clear adaptations to bipedalism, although they retained some arboreal features, such as long arms suited for climbing. The robust *Paranthropus* genus, showing specialized adaptations for heavy chewing, also appeared during this period, and persisted until around 1 Ma, well after the disappearance of the Australopithecines. The coexistence of multiple hominin species in Africa during this time underscores the diversity of evolutionary experiments in morphology and behavior, with each species probably occupying distinct ecological niches. However, taxonomic uncertainties persist, as the boundaries between some australopithecine and *Paranthropus* species remain fluid, leading to ongoing debates about their exact phylogenetic relationships (Wood and Boyle 2016).

Around 2.5 Ma, *Homo habilis* enters the fossil record, marking the emergence of the genus *Homo*, notably characterized by full bipedalism, large brain size, reduction of sexual dimorphism, and dentition (see Figure 2 below). The classification of *H. rudolfensis* is debated, with some researchers suggesting it could be a species distinct from *H. habilis* due to its unique combination of features, such as a larger brain and a more modern face. It is generally accepted that it was *H. habilis* that gave rise 1.8 Ma to *H. erectus* and *H. ergaster*. *H. ergaster* lived around 1.9 Ma to 600 Ka, primarily in East and South Africa. The distinction between *H. ergaster* and *H. erectus* is a subject of ongoing debate, with many researchers viewing *H. ergaster* as the African variant of *H. erectus* rather than a separate species (Antón et al. 2014). Others maintain that anatomical differences justify classifying *H. ergaster* as its own species. *H. georgicus* is an important, yet somewhat enigmatic, early human species, generally interpreted as representing a transitional form between *H. habilis* and *H. ergaster* or *H. erectus* (Lordkipanidze et al. 2013). Discovered at Dmanisi in Georgia, this species dates to around 1.8 million years ago, making it one of the earliest human species to be found outside Africa. The fossils from Dmanisi are highly significant because they reveal a combination of primitive and advanced traits. While *H. georgicus* had a relatively small brain size, similar to *H. habilis*, its body proportions were more modern, akin to *H. erectus*, suggesting adaptations for long-distance walking or running.

Approximately 1.8–1.6 Ma, *H. erectus* migrated from Africa to Eurasia, reaching as far as China and Indonesia, where it persisted for over a million years; although this does not imply that *H. erectus* remained genetically and phe-

notypically unchanged over this long period. Some African populations of *H. erectus* and *H. ergaster* are considered by many to be ancestral to later *Homo* species, including *H. heidelbergensis*, a descendant species that emerged around 600 Ka. From then on, human biocultural evolution in Africa was paralleled in other *Homo* species living in Eurasia, before their evolutionary trajectories were truncated, or more accurately, assimilated by anatomically modern human expansion from 60 Ka. *H. heidelbergensis* has been claimed to be the probable ancestor, c. 600–450 Ka, of Neanderthals and Denisovans in Eurasia. Others consider that *H. antecessor*, an early human species that lived approximately 1.2 Ma–800 Ka, primarily known from fossil remains found in the Atapuerca region of Spain, may have been an ancestor to *Homo heidelbergensis*, Neanderthals, and modern humans (Bermúdez de Castro et al. 1997; Lockey et al. 2022). *H. antecessor* exhibited a mix of primitive and advanced traits. Its facial anatomy, with a relatively flat face and modern-looking midface, shares features with both later hominins and modern humans, while other aspects, like its robust jaw and teeth, resemble earlier species. Paleoanthropologists generally do not consider that *H. erectus* migrated into Europe because the fossil evidence suggests that different hominin species, such as *H. antecessor* and later *H. heidelbergensis* occupied Europe during the time when *H. erectus* was widespread in Africa and Asia.

The separation between *H. sapiens* and their common ancestor with Neanderthals (*H. neanderthalensis*) and Denisovans is estimated based on genetic evidence to have occurred from around 400–500 Ka and, based on genetic evidence (Levinstein-Hallak and Rosset 2024), that between *H. sapiens* and Denisovans c. 1 Ma. The separation between Neanderthals and Denisovans is believed to have occurred around 600 Ka (Zeberg et al. 2024), although based on mitochondrial DNA analysis Levinstein-Hallak and Rosset (2024) date the divergence between modern humans and Neanderthals to ~400 Ka and that between modern humans and Denisovans to ~840 Ka. The separation between Neanderthals and Denisovans is believed to have occurred around 400 Ka to 450 Ka, after their common ancestor split from *H. sapiens*. This divergence is thought to have resulted from the isolation of two populations of a common ancestor, likely *H. heidelbergensis*, which was widespread across Africa and Eurasia during the Middle Pleistocene. These “isolations” were permeable. Recent studies (Li et al. 2024; Peyrégne et al. 2022; Reilly et al. 2022) reveal that interbreeding events between *H. sapiens* and Neanderthals occurred in multiple waves, challenging the previous notion of sporadic interactions after the split. Li et al. (2024) identify at least three major periods of gene flow—around 200–250 Ka, 100–120 Ka, and 50–60 Ka (see §3.6). This recurrent gene flow shows that migrating Africans were not only dispersing out of Africa but also returning and encountering Neanderthals multiple times throughout the Middle Paleolithic/Middle Stone Age. The findings highlight how these interactions affected both Neanderthals and African populations, influencing evolutionary dynamics. A notable aspect of this research is the reverse focus—examining modern

human DNA found in Neanderthal genomes—indicating that early modern humans left a genetic imprint on Neanderthals during these periods of contact. This ongoing gene flow likely had significant implications for both groups, contributing to the genetic diversity seen in modern humans today (Iasi et al. 2024).

Genetic studies have also demonstrated that modern human populations, particularly those from Southeast Asia, Melanesia, and Australia, carry a substantial percentage of Denisovan DNA. It is suggested that there were at least two significant episodes of gene flow, one around 100 Ka and another closer to 50 Ka, when *H. sapiens* populations encountered Denisovans after their migration out of Africa. The highest proportion of Denisovan DNA is found in Papuan and Australian Aboriginal populations (Jacobs et al. 2019). There is also strong evidence of gene flow between Neanderthals and Denisovans. Genomic analyses of remains from Denisova Cave in Siberia provide evidence of interbreeding between Neanderthals and Denisovans (Slon et al. 2018). This suggests that their populations interbred after the two groups diverged from a common ancestor around 400 Ka. The admixture events likely occurred in regions of Eurasia, where the ranges of Neanderthals and Denisovans overlapped.

Homo floresiensis, discovered on the Indonesian island of Flores, had a remarkably small brain and stood only about 3.5 feet tall (Brumm et al. 2016). An early form of *Homo floresiensis* might have existed on Flores as far back as 700,000 years ago (Van den Bergh et al. 2016a). Evidence comes from the Mata Menge site, where researchers found ancient teeth and a jaw fragment. These fossils, though more primitive than those found in the Liang Bua cave, where the classic *H. floresiensis* skeletons dated between 100 Ka and 60 Ka were unearthed, share key morphological features with *H. floresiensis*. This suggests a long-term presence of the species on Flores and potentially an extended period of isolation, leading to distinct adaptations like small body and brain size. Recent taphonomic analysis calls into question previous suggestions that this species was capable of complex behaviours involving the controlled use of fire and coordinated hunting of large animal prey (Veatch et al. 2026). *H. luzonensis* is a recently discovered hominin species identified from fossil remains found in Callao Cave on the island of Luzon in the Philippines (Détroit et al. 2019). These remains, dated to about 50 Ka to 67 Ka, include a mix of teeth and small bones from the hands and feet, displaying a combination of both modern and primitive traits. The species shows similarities with *Homo floresiensis*, particularly in its small size and some archaic features, despite the two species being separated by significant geographic and evolutionary distance.

In summary, before 100 Ka the evolution of our lineage was complex, and the taxonomy of fossil species itself is constantly evolving as a result of new discoveries, revised interpretations of ancient fossil remains, and new evidence provided by genetics and paleogenomics. In their synthesis on the dating of fossil human remains from the last million years, Grün and Stringer (2023) mention the presence dur-

ing this period of at least ten fossil species, some of which (such as *H. luzonensis*, *H. floresiensis* or *H. naledi*) are known only from fragmentary remains or from a single site. Others, such as the Denisovans, are well known in terms of their genome, but poorly known for their morphology. Neanderthals are by far the best represented fossil species in the paleontological record, with around 400 individuals and 30 relatively complete skeletons. For comparison, the total number of human remains indicating the emergence of anatomically modern humans in Africa before 100 Ka comprises around 20 to 25 individuals; and after 100 Ka 10 to 15 individuals, possibly more when taking into account small finds and fragmentary remains (Scerri et al. 2018; Stringer 2016).

3.2. THE CLIMATE RECORD

Over the 5 million years that have witnessed the evolution of the members of our lineage, the climate of our planet underwent significant changes, as recorded by benthic foraminifera oxygen isotope data (Figure 2). Overall, Earth's climate has shown a long-term trend toward cooling over the last 5 million years and shorter-term oscillations, increasing their frequency and amplitude over time. The trend culminated in the Quaternary period's frequent glacial cycles, characterized by stronger ice ages and greater millennial-scale climatic variability after 1 million years ago. During the Late Miocene (5.5 Ma to 5.3 Ma) the climate was warmer and more stable than today, with high temperatures and less ice coverage. A slight cooling started in the Late Miocene, continuing in the Pliocene (5.3 Ma to 2.6 Ma), with a particularly warm phase around 3.3 Ma, known as the Pliocene Warm Period, during which temperatures were about 2–3°C warmer than present. Ice sheets, particularly in the Northern Hemisphere, were significantly smaller. The Early Pleistocene (2.6 Ma to 1.2 Ma) marked a significant shift into cooler phases. The expansion of ice sheets, especially in the Northern Hemisphere, initiated glacial-interglacial cycles, characterized by periods of cold (glacial) conditions interrupted by shorter, warmer (interglacial) intervals. These cycles were primarily influenced by changes in Earth's axial tilt, leading to glacial cycles occurring every 41 Ky.

The Mid-Pleistocene Transition (MPT), marking the starting of Middle Pleistocene (1.2 Ma to 0.3 Ma), led to a major change in glacial cycle frequency and amplitude. After the MPT, glacial cycles extended to a 100,000-year rhythm, influenced by Earth's orbital eccentricity. This period was marked by larger ice sheets and more extreme cold phases, with pronounced glaciations and shorter, warmer interglacials. Throughout the Upper Pleistocene (0.3 Ma to 10 Ka), the amplitude of glacial-interglacial cycles intensified, with notable cold periods like Marine Isotope Stage 6 (190 Ka to 130 Ka) and warmer interglacials such as Marine Isotope Stage 5e (130 Ka to 115 Ka). The last glacial cycle culminated in the Last Glacial Maximum (around 20 Ka), followed by rapid deglaciation starting around 18 Ka and leading to a rapid warming phase that culminated in the onset of the Holocene around 10 Ka, marking the transition

to the stable, warm interglacial period we live in today. Researchers have repeatedly argued, although from different perspectives, that these climatic shifts had significant effects on hominin evolution (Behrensmeier 2006; deMenocal 2011; Potts and Faith 2015; Sánchez-Gómez 2020; Stibel 2023; Timmermann et al. 2024). Cooling trends, combined with more frequent glaciations and increasing climate variability, may have influenced key evolutionary events such as the development of bipedalism, brain expansion, and the spread of *Homo erectus* and *Homo sapiens* out of Africa. These environmental pressures may have driven the adaptation to changing habitats, the development of social and cultural innovations, and the consolidation and complexification of cumulative cultural evolution, leading to the gradual construction of more and more complex biocultural niches (Sterelny 2016).

3.3. MATERIAL CULTURE: THE LITHIC RECORD

3.3.1. Earliest Steps in Tool Manufacture and Use

Recent discoveries support a long term, multispecies, gradual and polycentric process of the construction of diverse biocultural niches by *Homo sapiens* and related lineages. There is no one-to-one correspondence between material culture and fossil species, and a relatively high degree of variability is observed between artifacts attributed to the same stone tool industry. Archaeologists distinguish three broad cultural categories. The Oldowan, or Mode 1, between 2.9 and 1.7 Ma, was characterized by knapped pebble tools and simple flakes. The Acheulean, or Mode 2, from 1.6 Ma to 130 Ka, featured increasingly refined bifacially shaped large stone tools. From 400 Ka to 40 Ka, Mode 3 was characterized by retouched or unretouched flakes produced from prepared cores allowing a degree of planning of the flake morphology. Figure 2 provides timelines for the fossil record of principal human ancestors over the last 2 million years, the periodization of main cultural adaptations in Africa and Eurasia, and a curve illustrating the evolution of climate at a global scale.

The earliest knapped stone tools date back to 3.3 Ma, predating by 500,000 years the earliest remains of representatives of the genus *Homo*, and extending the record of hominin technology by some 700,000 years compared to earlier findings. These early lithic industries, called Lomekwian from the Kenyan site where they were discovered (Harmand et al. 2015), were probably created by members of the genus *Australopithecus* or *Kenyanthropus*. Refitting of lithic artifacts from the 2.34 Ma Kenyan site of Lokalelei has shown that production of standardized flakes necessitated careful planning, entailing judgements of initial size and affordances, the sequential planning of multiple successive actions to remove similar sized flakes, and correction of knapping errors. The Oldowan, once thought to be the earliest stone tool industry, dating from around 2.6 to 1.7 Ma, was characterized by choppers and simple flakes produced by striking a lithic hammer against a suitable rock. These tools allowed hominins to process animal carcasses,

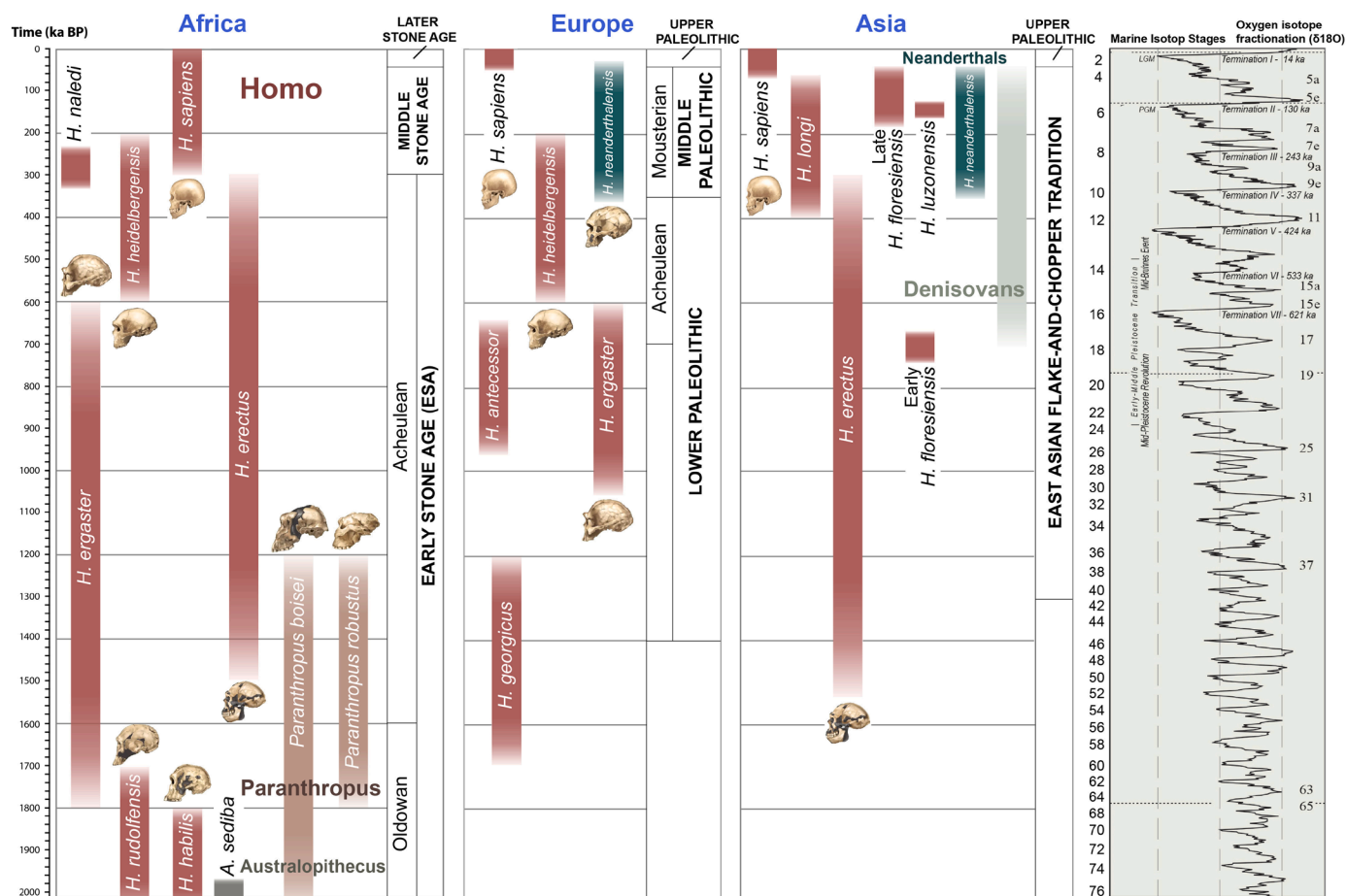


Figure 2. Timelines for the fossil record of principal human ancestors over the last 2 million years, the periodization of main cultural adaptations in Africa and Eurasia, and a curve illustrating the evolution of climate at a global scale, indicating the gradual reduction in temperature associated with an increase in the amplitude of climatic fluctuations at the Middle-Upper Pleistocene transition, c. 1.2 Ma to 600 ka. See text for detailed explanation on hominin types, cultural adaptation, and climate change (compiled from various sources; climate curve from Cohen and Gibbard 2010. Drawing by Lila Geis).

cut meat, and process plant materials. The attribution of the Oldowan to specific hominin species is a subject of ongoing debate due to the overlapping presence of several hominins during this period, namely *H. habilis*, *Australopithecus*, *Paranthropus*, and *H. ergaster* and the likelihood that multiple hominin species were using this technology either independently or through cultural transmission. Oldowan (Mode 1) technology was previously thought to have originated in East Africa about 2.6 Ma. However, it is now firmly attested at nearly contemporaneous sites dated to 2.4 Ma in North Africa (Sahnouni et al. 2002) and possibly in Asia.

Contrary to long-held assumptions that Oldowan technology displayed no major variation over a span of 2 million years, we now know that high variability characterized Oldowan industries since their very beginning. Several researchers (Harmand et al. 2015; Delagnes and Roche 2005; de la Torre et al. 2011; Toth 1985) have highlighted the variability in Oldowan assemblages, especially the differences in raw material use, tool types, and production strategies, suggesting regional distinctions in tool-making approach-

es. They note that while the basic core-flake reduction system is consistent, local adaptations and technological innovations reflect possible cultural differences between groups of early hominins and knapping strategies of varied complexity and cognitive demands. These differences are likely to be due to cumulative cultural diversity, possibly reflecting different modes of social learning and cultural transmission strategies, but did not lead to an archaeologically detectable cumulative increase in technological complexity.³

Outside Africa, the antiquity of stone tools and the anatomical features of the earliest skeletal remains challenge the assumed link between the African origins of *Homo erectus* about 2–1.8 Ma, and the makers of the earliest flaked industries found in Eurasia. The site at Shangchen, Chinese Loess Plateau, has yielded possible knapped stone tools in layers dated to 2.1 Ma (Zhu et al. 2018). The earliest skeletal evidence for the genus *Homo* in Eurasia, displaying anatomical features closer to *Homo habilis* than to *H. erectus*, named *H. georgicus*, is from Dmanisi in modern-day Geor-

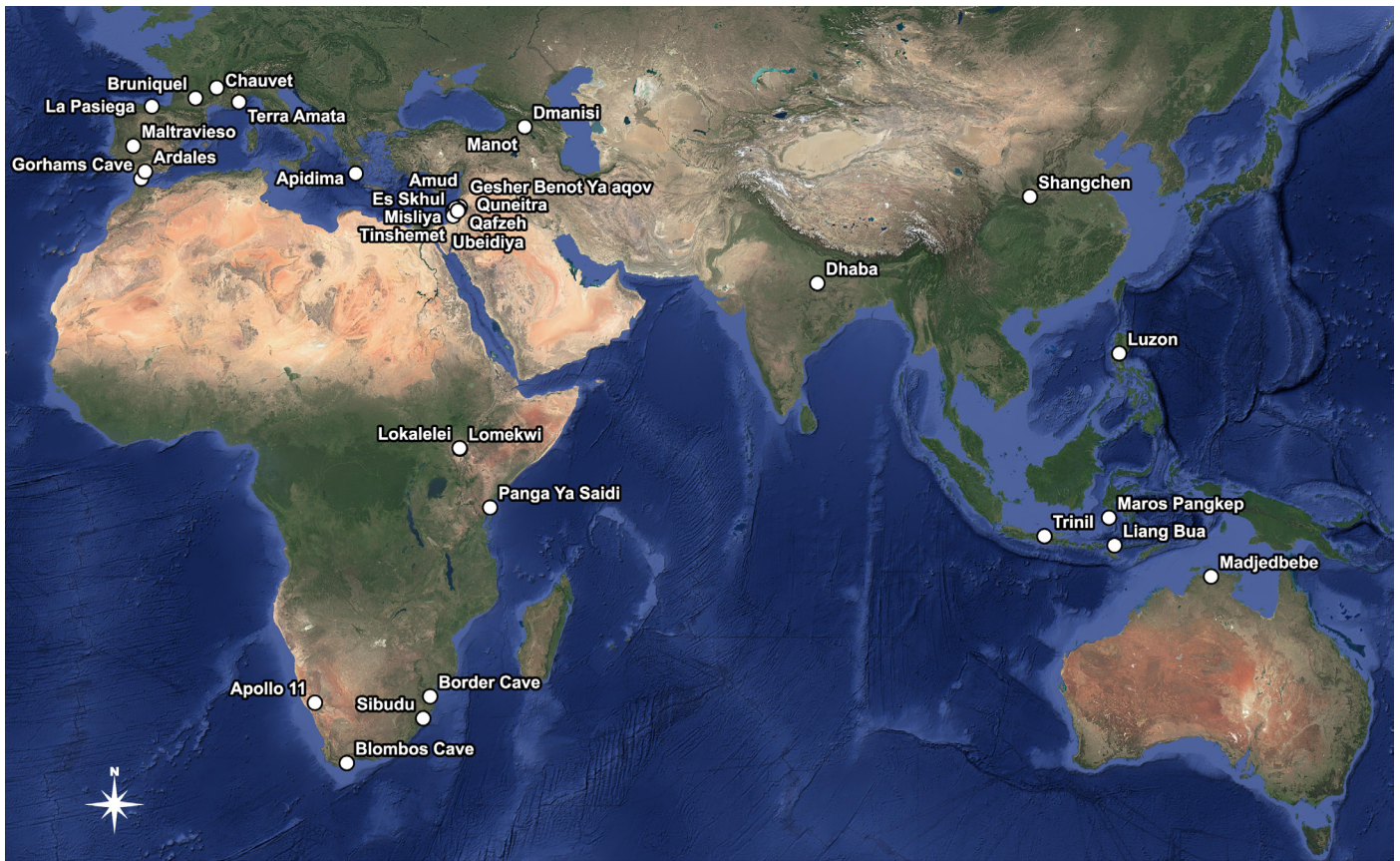


Figure 3. Locations of archaeological and paleontological sites referred to in this publication (drawing by Lila Geis).

gia, and is dated to c. 1.7–1.8 Ma, implying an earlier dispersal through (at least) the Near East. Equally significant are Levantine sites such as ‘Ubeidiya (Israel), dated to ca. 1.5 Ma, which has yielded a rich early Acheulean assemblage (Bar-Yosef and Belmaker 2017; Bar-Yosef and Goren-Inbar 1993; Herzlinger et al. 2021). Even earlier evidence for hominin presence in Jordan, probably older than 2 Ma, has been reported (Scardia et al. 2019). These discoveries highlight the Levant as a major corridor for early Out-of-Africa dispersals.

In sum, current evidence suggests that the expansion of the genus *Homo* outside Africa may have been a gradual, stepwise process, with niche expansion and geographical range incrementally extending over time, rather than resulting from a single, large-scale migration event linked to the expansion of *H. erectus* or *H. ergaster*; and that earlier *Homo* populations were responsible for much of the niche expansion traditionally attributed to the *H. erectus-ergaster* lineages. Figure 3 maps the archaeological sites referred to above and in the remainder of the paper.

3.3.2. The Acheulean Expansion and the Earliest Sea Crossings

From around 1.76 Ma [shown as 1.6 in Figure 2] we see, in East Africa, the earliest instances of Acheulean (Mode 2) bifaces (Lepre et al. 2011). Only from 1.0–0.7 Ma do we

see bearers of this technology disperse out of Africa, in southern Europe, across western Asia, and into South Asia (de la Torre 2016). In the Levant, the Acheulean record includes the remarkable site of Gesher Benot Ya’aqov (Israel), which preserves not only Acheulean lithic industries but also rare wooden implements (Goren-Inbar et al. 2000; 2002). At this site, some of the earliest secure evidence for the controlled use of fire has been documented, alongside indications of aquatic plant exploitation (Goren-Inbar et al. 2004; Melamed et al. 2016). These finds testify to innovative ecological niche expansion in the Levantine corridor, reinforcing its role as a hotspot for behavioral advances during the Acheulean. The populations migrating during the two earliest known Out-of-Africa dispersals, (*H. habilis/georgicus* around 1.8 Ma and *H. ergaster* around 1.2 Ma were not bearers of Acheulean but rather of Mode 1 technologies. They were able to adapt to new and often challenging environments in a process of niche expansion. This entailed discovering new sources of lithic raw material and transmitting information about their location and quality to new generations; sharing information on the seasonal movements of hunted species, elaborating novel hunting techniques adapted to a variety of new prey, creating or improving some form of clothing to cope with seasonally contrasted climates, and establishing a degree of cooperation required, for example, to butcher and consume large

herbivores or defend against predators occupying the same ecological niches. These eco-biocultural innovations are markedly different from those observed in present day non-human primates (Bandini and Harrison 2020; Vale et al. 2021).

Although the dating of the first colonization of Europe (as distinct from the evidence for *H. georgicus* in Eurasia) remains controversial, it is only at c. 1.2 Ma that we find hominin remains and diagnostic stone tools in southern Europe. Acheulean technology appears in the Iberian Peninsula around 1 Ma, but there is no evidence for it in France and Italy before 0.7 Ma, or in northern Europe before 0.5 Ma; this suggests an arrival from Africa through the strait of Gibraltar. An African provenance of the Iberian Acheulean is also supported by the significant proportion of large U-shaped tools with a distal cutting edge, called cleavers, which are preferentially shaped at these early sites on large cortical flakes. Such artifacts are extremely rare at more recent sites in the remainder of Europe, but are characteristic of the contemporaneous Northern Africa Acheulean (Méndez-Quintas et al. 2018; Santonja and Villa 2006; Santonja et al. 2016; Sharon and Barsky 2016).

The mastery of fire would have provided an obvious advantage for the expansion and settlement of African populations into Asia, but archaeological evidence attesting to the emergence of this innovation has traditionally been seen as scant and controversial (Roebroeks and Villa 2011). While the sites of Xihoudu, Majuangou, and Yuanmou, dated to between 1.7 and 1.2 Ma, provide some of the earliest potential evidence for fire use by hominins in Asia, the findings remain contentious (Chazan 2017; Goldberg et al. 2017). Evidence for hominin clothing use around 700 Ka is largely circumstantial. Sites from this and more recent periods contain stone tools and animal remains with cut marks, indicating that early humans processed animal hides. However, diagnostic use wear and micro residues indicating hides processed by stone tools are not detected before 400 Ka (Gilligan et al. 2024).

Differences in chronology and location of the earliest seafaring suggest that it emerged in a polycentric manner, being invented independently in different regions according to local conditions and needs. The colonization of off-shore islands in Wallacea is widely recognized as one of the most striking markers of advanced cognitive, technological, and social capacities in early hominins (Anderson 2010; Napolitano et al. 2021). The crossing of a sea gap of at least 19 km between Bali and Lombok, Indonesia, occurred by at least approximately 1 Ma, as indicated by the earliest stone tools found on Flores (Brumm et al. 2010; Van den Bergh et al. 2016b). The discovery of a 777–631 Ka butchery site associated with stone tools in Luzon (Philippines) implies that Middle Pleistocene hominins crossed the Luzon and Mindoro Straits well before the colonization of this archipelago by more recent human populations (Ingicco et al. 2018). New discoveries from Sulawesi push this record even further back—Hakim et al. (2025) report stone artifacts from Calio in the Walanae Depression, securely dated to at least 1.04 Ma and possibly up to 1.48 Ma. These findings indicate

that archaic hominins were able to cross substantial ocean barriers in Wallacea more than a million years ago, contemporaneously with or earlier than those reaching Flores, making Sulawesi one of the earliest documented cases of hominin seafaring.

Evidence of crossing of the Mediterranean open sea by Neanderthals before the arrival in Europe of *H. sapiens* comes from several Greek islands and Corsica (Gaffney 2021; Galanidou et al. 2016; Howitt-Marshall and Runnels 2016; Runnels 2014). Lower and Middle Paleolithic sites found in these islands, in some cases going back to 130 Ka and possibly 250 Ka, show that Neanderthal populations living in Europe had the cognitive and technological abilities to produce watercraft for open-sea crossings. The first human occupation of the British Isles occurred between ca. 1 Ma and 0.78 Ma, but owing to sea levels lower than those of today this did not require sea crossing and is associated with simple Mode 1 flake technology (Ashton et al. 2014; de Groote et al. 2018; Parfitt et al. 2010). The evidence therefore supports the idea of a diverse and adaptable set of pathways for the development and spread of early human technologies. In order to develop, maintain, and adapt along their dispersal the multifaceted array of behavioral innovations necessary to cross these straits, the early voyagers must surely have had relatively sophisticated ways of communicating, involving communicative symbolic representation, though not necessarily by means of EMLs.

3.3.3. The Emergence and Development of Distinct Technocomplexes

Mode 3 lithic industries are largely synonymous in Africa with the Middle Stone Age (MSA) (350–40 Ka), and in Europe and western Asia with the Mousterian industries (350–40 Ka) generally assumed to be associated with Neanderthals. The beginning of the MSA in Africa is characterized by a gradual shift from the large bifacial cutting tools typical of the Acheulean to removing flakes from cores, termed Levallois, in which the morphology and size of the desired end-product are determined by the ordered and controlled detachment of previous flakes (Deino et al. 2018; Douze and Delagnes 2016). Some of these flakes were re-touched and probably hafted from the very beginning of this period if not earlier (Wilkins et al. 2012; see Arbib et al. 2023 for a discussion of the significance of the transition from subtractive to additive tool construction). Since this innovation is found in widely dispersed regions of Eurasia, without its point (or points) of origin being known (Adler et al. 2014; Li et al. 2019), it cannot be interpreted as reflecting a successful expansion of early “modern” populations within or beyond the African continent, nor as supporting a decisive cognitive divide between African and non-African populations in the 300–100 Ka time range.

The presence of Mode 3 technology in widely dispersed regions suggests that it either developed independently in multiple locations or, less probably, spread rapidly across these areas, pointing to a convergent evolution of cognitive skills among different populations, reflecting parallel developments rather than diffusion from a single point of

origin. This could have been facilitated by occasional interactions and gene flow between groups, leading to a shared technological knowledge base without necessitating a diffusion scenario. Levallois technology requires precise planning and execution guided by teaching and learning the steps of flake production. We address in HOLO 2 (Arbib et al. 2027 [this issue]) the implications of this for the evolution of structural complexity of communicative systems in their social context.

After c. 150 Ka, Mode 3 technologies from some regions of Africa and Europe regionally diversify and give rise, between 150 Ka and 40 Ka, to spatio-temporally differentiated *technocomplexes*, characterized by distinct knapping techniques, stone tools, and, in some cases, bone tools and symbolic productions. Distinct African technocomplexes can be recognized from 140 Ka in North Africa, with the Aterian technology (Doerschner et al. 2016; Scerri et al. 2018), and in Southern Africa with the Pietersburg, and subsequently the Still Bay and the Howiesons Poort technologies (d’Errico et al. 2018; de la Peña et al. 2018; Porraz et al. 2018). In some African regions, Middle Stone Age lithic technologies gave way, after 50–40 Ka, to sometimes more complex, sometimes simpler Later Stone Age technologies (Backwell et al. 2018; Bousman and Brink 2018; Burrough et al. 2019; Loftus et al. 2016; 2019; Scerri et al. 2018; Soriano et al. 2007; Tryon et al. 2018; Villa et al. 2012; Wurz 2019), while in others, MSA technologies persisted (Scerri et al. 2018). Less preplanned, and rarely retouched, flake and core technologies persist until 40 Ka in East Asia. It is only after 90 Ka, perhaps earlier, that the first instances of fully shaped bone tools are found in northern and southern Africa (Backwell and d’Errico 2016; Bouzouggar et al. 2018; d’Errico and Henshilwood 2007; d’Errico et al. 2012). They remain absent or only emerge between 10 to 50 Ka later in other regions of Africa, a time range in which these technologies were widespread in Eurasia (d’Errico et al. 2020).

3.4. DENISOVANS AND NEANDERTHALS: ORIGINS AND GENE SURVIVAL

Before exploring the emergence of *Homo sapiens* in Africa and their subsequent spread into Eurasia, we review evidence referring to the archaic hominins that colonized Europe and Asia long before they did. Genetic evidence indicates that different populations of these earlier hominins became isolated, giving rise to at least two separate lineages that led to Neanderthals and Denisovans (Meyer et al. 2012; Slon et al. 2018; Reich et al. 2010). The split between these two populations would have occurred either c. 600 Ka (Reich et al. 2010) or 370–440 Ka (Petr et al. 2020; Prüfer et al. 2017). Both periods were marked by the southernmost extension of the ice-sheets, with permafrost probably developing as far south as the Black Sea (Sánchez-Gómez 2020), leading to an ice barrier separating Neanderthals in the west and Denisovans in the east, with subsequent genetic drift (see Figure 2). Recent genomic discoveries point to complex structuring of Denisovan populations (Browning et al. 2018), with multiple introgressions of Denisovan genes (3–5%) detectable in present-day Papuan and East

Asia populations. Papuans carry hundreds of gene variants from two divergent Denisovan lineages that separated over 350 Ka. The introgression from one of these lineages apparently continued until close to the end of the Pleistocene, 12 Ka. An introgression from a third Denisovan lineage is found in present-day East Asians (Massilani et al. 2020). Apparently, *Homo sapiens* repeatedly came into contact and interbred, in some cases over long periods of time and until relatively recently, with multiple, geographically isolated, Denisovan groups (Jacobs et al. 2019).

Paleoanthropological evidence suggests that archaic hominins living in Europe slowly acquired typical Neanderthal features during the late Middle and early Upper Pleistocene, i.e., 400–120 Ka. During this period, pre-Neanderthal and Neanderthal ranges fluctuated, with populations intermittently occupying regions such as the British Isles, the Near East, western Asia, and possibly more northern latitudes (Benito et al. 2017; Blinkhorn et al. 2021; Krause et al. 2007; Li et al. 2018; Yousefi et al. 2020). Modern humans repeatedly came into contact and interbred with Neanderthal and Denisovan groups, with 1–2% of genes in today’s humans being Neanderthal in origin.

The diversity of Neanderthal cultural practices established in regions of Europe before any contact with *Homo sapiens* included complex and changing lithic technologies including blade production (Delagnes and Rendu 2011; Delagnes et al. 2007; Morin et al. 2014), manufacture of wooden, sea shell and bone tools (Douka and Spinapolice, 2012; Van Kolfschoten et al. 2015), mastery of fiber technology (Hardy et al. 2020), ability to organize their living space (Alperson-Afil and Hovers 2005; Gabucio et al. 2014; Spagnolo et al. 2019), widespread use of medicinal plants (Hardy 2022), and healthcare not distinctively different from the healthcare practices of *H. sapiens* during the Upper Paleolithic and the Mesolithic (Spikins et al. 2018). These practices are indicative of strong pro-social bonds, the capacity to respond to climate change with technological shifts (Banks et al. 2021), hafting techniques involving the preparation of glues and adhesive compounds (Barham 2013; Degano et al. 2019; Koller et al. 2001; Kozowyk et al. 2017; Niekus et al. 2019), varied hunting strategies enabling Neanderthals to kill dangerous game (Niven et al. 2012), exploitation of a variety of marine (Stringer et al. 2008; Zilhão et al. 2020) and plant resources (Hardy and Moncel 2011; Henry et al. 2011; Power et al. 2018), and the established ability to ignite and control fire (Aranguren et al. 2018; Henry 2017; Vidal-Matutano et al. 2019).

3.5. THE AFRICAN MOSAIC: EMERGENCE OF *HOMO SAPIENS*

For decades, it was widely accepted that all *Homo sapiens* populations descended from a single group living in Africa some 200 Ka, who diverged from other lineages and migrated “Out of Africa” in a single event about 60 Ka (Cann et al. 1987; but see McBrearty and Brooks 2000 for an early critique). Human remains such as those found at Herto and Kibish, in Ethiopia, dated between 150 Ka and 200 Ka, were considered the earliest fossil instances of this original

anatomically modern humanity (Clark et al. 2003; Stringer 2002). In this view, these populations were endowed with a distinct cranial morphology supporting a packet of novel and modern cognitive capacities. This new species was seen as having rapidly replaced, without notable genetic or cultural exchange, other (archaic) African populations (Klein 1995; Relethford and Harpending 1994).

However, critical analysis (Scerri et al. 2018; Storz and Beaumont 2002; Wakeley 1999) of past approaches used by geneticists to identify population splits and infer their timing shows that they neglected factors such as population structure, changes in population size, and gene flow. Studies taking these factors into account, as well as a growing body of past genomic data (Durvasula and Sankararaman 2020; Patin and Quintana-Murci 2018; Wolf and Akey 2018), converge with the conclusions of paleoanthropological reappraisals of the fossil evidence—namely that evolution in diverse distinct but interacting populations, retaining the signature of a very ancient human ancestry, can better account for current genetic variability. This new scenario is also consistent with evidence demonstrating genetic admixture between archaic hominins and modern populations expanding out of Africa (Browning et al. 2018; Fu et al. 2015; Gunz et al. 2019; Harris and Nielsen 2016; Slon et al. 2018; Schlebusch et al. 2017). There is no reason to think that similar processes of hybridization should not have also taken place within Africa. Indeed, recent genetic studies increasingly support the view that population contact and hybridization were recurrent within Africa as well. Evidence of deep population structure and recurrent gene flow among early African populations points to a reticulate rather than linear model of modern human origins (Henn et al. 2018; Scerri et al. 2018; Schlebusch et al. 2017). These findings underline that hybridization within Africa was likely as significant as interbreeding events documented outside Africa, further reinforcing our polycentric perspective on biocultural niche expansion.

Data on genetic and phenotypic variability also contradict the hypothesis that present-day humans descended from a unique ancestral population occupying either eastern or southern Africa (Henn et al. 2012; but see Chan et al. 2019 and Rito et al. 2019 for an update of this view). Gene exchange left permanent traces in the cranial morphology of non-African modern humans (Dannemann and Kelso 2017; Gregory et al. 2017; Günz et al. 2019), on the functional connectivity of the modern human brain (Gregory et al. 2021), and on gene regulation (Dannemann et al. 2017). It is now accepted that anatomical traits that distinguish our cranial morphology from that of our archaic African ancestors emerged gradually, in Africa, between 300 Ka and 35 Ka, with present-day human morphological variation attained only in the time span of 100 Ka to 35 Ka (Bergström et al. 2021; Gunz et al. 2009; Hublin et al. 2017; Neubauer et al. 2018; Scerri et al. 2018). In other words, neither paleoanthropology nor paleogenomics support a clear distinction between a ‘before’ (“archaic”) and an ‘after’ (“modern”). Instead, we see, starting from 300 Ka, the emergence of associated modern and archaic characters in populations

scattered throughout Africa.

The morphological variability, chronology, and geographical distribution of the first fossils now attributed to *Homo sapiens* suggest relatively independent processes co-occurring in several different African regions (Scerri et al. 2018). Although some scholars continue to argue for a sharper distinction between ‘archaic’ and ‘modern’ humans, often framed within a debate between Pan-African and single-origin models of *Homo sapiens* (Meneganzin et al. 2022), we consider the growing body of genetic, fossil, and archaeological evidence for deep population structure, recurrent gene flow, and regional variation to be more consistent with a graded, polycentric model of biocultural evolution rather than with a binary division between ‘archaic’ and ‘modern’.

3.6. *HOMO SAPIENS* EXPANSION OUT OF AFRICA

The tempo and mode of modern human expansion out of Africa are highly debated issues, particularly in relation to genetic and cultural contact with the already existing Eurasian populations. The traditional view envisaged occasional expansions limited to the Near East starting 180 Ka, occurring before a widespread colonization of Asia and Wallacea c. 60–50 Ka and of Europe c. 40 Ka. This has been challenged by genetic evidence (Kuhlwilm et al. 2016; Paganini et al. 2016), discoveries of more ancient human fossils attributed to “modern” humans, and archaeological remains interpreted as proxies of a modern human colonization at pre-60 Ka sites. An early dispersal of modern humans into the Near East is inferred from the discovery of a mandible dated to 177–194 Ka at the Misliya Cave in Israel (Hershkovitz et al. 2018). An even earlier modern human presence in Europe, at 210 Ka, has been proposed, based on the morphology of a human cranium from the Apidima Cave, Greece (Harvati et al. 2019).

A human phalange from a site in the Arabian Peninsula (Groucutt et al. 2018), remains from four sites in southern China (Huanglong, Zhiren, Luna, Fuyan) (Dennell et al. 2020), and human teeth from Sumatra (Westaway et al. 2017) have also been interpreted as evidence of precocious “modern” human dispersals in these regions, respectively 85 Ka, 120 Ka and 73–63 Ka. An early and persistent “modern” human presence in South Asia, starting 79–65 Ka, has been argued for on the basis of similarities between lithic technologies found at the site of Dhaba, Central India, and contemporaneous African Middle Stone Age sites (Clarkson et al. 2020). Recent finds from Madjedbebe, northern Australia, have also been interpreted as attesting a “modern” human colonization of this continent around 65±6 Ka (Clarkson et al. 2017).

Although an early dispersal into Asia of African populations much older than 60 Ka is perfectly plausible, and supported by modelling approaches (Wakano and Kadowaki 2021) and by genetic data (Reyes-Centeno et al. 2014), much evidence in support of it is circumstantial (Hublin 2021; O’Connell et al. 2018). Archaeological and genetic evidence point to an arrival of modern populations

in Siberia and northern China around 45 Ka (Yang et al. 2024). New dating results and genetic analyses have shaken the foundations of previous interpretations of purportedly old human remains from southern China (Sun et al. 2021). Further uncertainty is introduced by the reanalysis of fossils such as Yunxian 2 (Feng et al. 2025), whose mosaic morphology has been variously attributed to late *H. erectus*, a population related to Denisovans, or a distinct archaic lineage, highlighting the difficulty of aligning fossil and genetic signals. Additional debates surrounding the taxonomic status of so-called “*Homo longi*” fossils further illustrate the unsettled nature of the Asian Middle Pleistocene record. It is, therefore, too early to establish with confidence a reliable scenario for the dispersal of modern populations throughout Asia. Available data point to a complex process that probably involved multiple dispersal events resulting in some cases in rapid expansion and replacement of local populations and in others long-term coexistence, leading to cultural exchange and interbreeding, with some regions colonized quite recently compared to others (Yang et al. 2024; 2025).

Despite enhancement of the spatial and temporal resolution of the mapping of late Neanderthal and *H. sapiens* distribution, due to the greater number of investigated sites and recovered human remains, the chronology of the arrival of modern populations in Europe and their interactions with European Neanderthals is not fully resolved. Some propose that episodic incursions of anatomically modern humans occurred in Western Europe as early as 54 Ka (Slimak et al. 2022, but see Zilhão et al. 2024). This claim, however, is for the moment supported only by evidence from a single site and a fragmentary human tooth. Modern humans associated with Initial Upper Paleolithic artifacts (blades detached from prismatic cores and bladelets) may have been present at Bacho Kiro, Bulgaria, 45 Ka (Hublin et al. 2020, but see Zilhão et al. 2024). In Western Europe, a pivotal moment in this process was the period around 42 Ka. This is when the so called Proto-Aurignacian archaeological culture (Banks et al. 2013; Bon 2006), often considered as the cultural proxy for a first main expansion of modern populations, spread to a large part of southern Europe (Banks et al. 2013; Chu and Richter 2020; d’Errico and Banks 2015). Another pivotal moment may have coincided with the spread over a wider part of Europe and the western Asia of the so called Ancient Aurignacian, ca. 40–38 Ka (Chu and Richter 2020; Zilhão and d’Errico 1999). These two closely related technocomplexes feature distinct knapping techniques for the production of lithic blades and bladelets, differing from each other in lithic and osseous tool types. Although present in both archaeological cultures, semiotic (as opposed to utilitarian) artifacts⁴ are more abundant in the Ancient Aurignacian. While the Protoaurignacian yields personal ornaments and a limited range of bone tools, the Ancient Aurignacian is characterized by complex and systematic osseous technology, including split-based points, as well as the first unambiguous figurative art, including ivory animal and human representations, often decorated with abstract engravings (Dutkiewicz 2021) and

cave art, as exemplified at Chauvet (Geneste et al. 2025).

There is ongoing debate regarding the taxonomic affiliation of the hominins responsible for the archaeological cultures of the Middle-to-Upper Paleolithic Transition. This includes discussions about the ProtoAurignacian in Southern Europe, the Châtelperronian culture in France and the Iberian Peninsula, as well as the Uluzzian culture in Italy and Greece. The innovations (ornaments, pigments, specialized bone and ivory tools) that these cultures manifested (see §4) were absent, or only sporadically present, in the earlier Neanderthal cultures. Their association with these technocomplexes has been variously interpreted as innovations brought to Europe by modern humans, the result of contact between Neanderthals and incoming modern humans, as autonomous cultural developments in Neanderthals, or as the consequence of a cultural explosion that took off between both populations. Some scholars have argued that some of these cultures, such as the Uluzzian, did not belong to Neanderthals and have interpreted these cultural adaptations as reflecting a more ancient colonization of Europe by *H. sapiens* prior to the Proto-Aurignacian. This proposal is undermined, however, both by the uncertain stratigraphic origin and fragmentary nature of the human remains on which it is based, and by the clear evidence from some sites, such as the Grotte du Renne in France, that the relevant artifacts were made by Neanderthals. A Neanderthal attribution of Châtelperronian material culture is also indicated by the fact that it features bone tools (*lissoirs*) and ornaments (raptor talons) found at Neanderthal sites much older than the attested arrival of *H. sapiens* on European territory. This strongly suggests (as already noted in §3.3) that late populations of Neanderthals in some regions of Europe produced a material culture comparable in complexity with that attributed to *H. sapiens* in Africa after 100 Ka (see §4).

In summary, evidence from archaeology, paleoanthropology, and genetics enables us to identify major transitions in the last three million years, from the emergence of the hominin line in Africa to the subsequent diversification of *Homo* populations. While current evidence continues to support a general “Out-of-Africa” scenario, it suggests that rather than *H. sapiens* being the result of a single speciation event occurring around 200 Ka, our species emerged over a longer period, with implicated groups living in different parts of Africa (e.g., Bergström et al. 2020; Scerri and Will 2023). Taken together, these findings challenge the representation of speciation as involving ever-more fine-grained branching leading to a unique terminus, suggesting instead an interweaving process resulting in a capillary-like structure of interaction, within a mosaic of coeval, co-evolving groups.

3.7. NEANDERTHAL GENE ASSIMILATION, CULTURAL CONTACT, AND COMMUNICATION

In light of the above, Zilhão et al. (2024) argue for a paradigm shift in this debate, criticizing the way that the concepts of “modern” and “archaic” are conflated across the fields of

paleoanthropology and genetics, despite fundamental differences in how these disciplines categorize them. Paleoanthropology relies on skeletal features that change over long geological timescales, while genomics examines changes in DNA over much shorter generational timescales. This discrepancy poses a challenge to understanding the interactions between Neanderthals and modern humans between 45 Ka and 35 Ka in Africa and western Eurasia.

The genetic evidence from Eurasian fossils dating to this period shows that fossils considered genetically modern often had Neanderthal ancestors within just a few generations, blurring the line between the two groups and indicating that genetic boundaries were far more fluid, further challenging the notion that differences in material culture or skeletal morphology directly correspond to clear distinctions between hominin populations. Accumulating evidence of widespread genetic exchange (Hajdinjak et al. 2021; Lalueza-Fox 2021; Slon et al. 2018) contradicts the attribution of this or that cultural trait to one or other genetically distinct human population. The traces of gene exchanges, clearly visible in the genome of modern non-African populations, confirm that individuals resulting from interbreeding were integrated into the *H. sapiens* societies of that time. In place of the popular image of the extinction of Neanderthals as a species, we can better conceptualize this process as involving the gradual disappearance of distinct Neanderthal ecocultural niches over a time span of two to three thousand years, probably between 43 Ka and 40 Ka, accompanied by the assimilation of some features of Neanderthal biology into a hybrid population in a number of novel biocultural niches.

In summary, convergent archaeological, paleoanthropological, and genetic evidence lead us to reject the notion of a single speciation event in Africa leading to a modern *Homo sapiens* that decisively replaced other *Homo* populations. Rather, the evidence supports a complex of genetic changes in populations inside Africa, with migrations yielding further variations through interaction with populations of *Homo* already established outside Africa. In the light of these considerations, many human remains classified in the past as belonging to distinct fossil species (Walker et al. 2024) can now better be interpreted as representatives of a polymorphic population of a single evolving biological species, phenogenotypically evolving in and with diverse biocultural niches.

The picture emerging from recent archaeological and genetic data, then, is one of prolonged contact between “modern” human populations arriving in Europe and Neanderthals, giving rise to genetic hybridization that most likely went hand-in-hand with cultural hybridization and syncretism, inter-cultural communication, and technological innovations. As we document in §4, cultural innovations over this long period included significant developments in semiotic artifacts and their associated practices. We can reasonably infer that inter-individual and inter-group communicative interactions also led to mixing between symbolic communication systems and artifacts. The challenge is to construct a coherent and plausible account of the re-

lationship between the increasing complexity of material artifacts retrieved from the archaeological record, and the origins and evolution of language. If we regard language as one among a variety of human symbolic constructions and vehicles, then we need a definition of symbolization that can encompass the diverse range of symbols and symbol systems, while distinguishing symbolic from non-symbolic artifacts and vehicles of communication.

4. MATERIALITY AND MEANING-MAKING

4.1. IN SEARCH OF THE SYMBOL

Since we cannot directly observe speech or manual sign, or hypothesized precursors such as pantomime (see HOLO 2: Arbib et al. 2027 [this issue]), we need to interrogate the archaeological record for material objects that (ideally) *must*, or (less securely) *may* have necessitated not only a potential symbolic cognitive capacity, but a semiotic niche within which conventional meanings were shared. These objects may then be treated as proxies for the existence of a semiotic niche, *but this does not mean that they are proxies for the existence of Evolutionary Modern Languages*. Humans are often described as the “symbolic species” (Deacon 1997). Yet despite the centrality of symbols in discussions of human evolution, there is little consensus on what constitutes a symbolic sign, how symbolization relates to language, or how symbolic behavior can be inferred from archaeological evidence (Currie et al. 2024; Hovers and Belfer-Cohen 2024). Language is the most complex symbolic system known, but symbolic practices are not restricted to language. Body ornaments, pigments, engravings, figurative images, and structured mortuary behaviors may also function as symbolic signs, provided they participate in shared systems of meaning. At the same time, the presence of such artifacts does not automatically imply fully developed language. Symbolic material culture and linguistic communication should be understood as co-evolving components of an expanding semiosphere, rather than as clearly demarcated thresholds (d’Errico et al. 2026).

Terms such as symbol, symbolic, and symbolism are frequently used in a broad and ill-defined sense, creating ambiguity about what kinds of cognitive and communicative capacities are being attributed to past populations. A comprehensive treatment lies beyond the scope of the present article. Our aim here is to outline a theoretical framework sufficient for clarifying how we use the terms symbol and symbolic, and for grounding the archaeological inferences developed below. The fundamental distinction that informs our approach is between *signals* and *symbols* (Bühler 2011; Maynard-Smith and Harper 2003; Sinha 2004). Maynard-Smith and Harper (2003: 3) define a signal as “any act or structure, which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved”. Signals are therefore communicative behaviors that convey relatively fixed information, usually having the function of prompting behavioral responses on the part of the receiver, such as is the case for animal alarm calls. Sig-

nals are ubiquitous in animal communication (Griebel and Oller 2024), and also occur in many modalities of natural and artifactually mediated human communication, for example, in “body language,” or traffic signals. In contrast with signals, symbols (and symbolic expressions) depend upon a mutual understanding by participants in communicative practices of a relationship between sign and referent within the communicatively established context, and they are *about* situations and events (Arbib 2021). Above all, symbols *represent* something outside the sign itself. Conventional symbol systems, such as language, are grounded in an intersubjective meaning-field in which speakers represent, through symbolic action, some segment or aspect of reality for hearers. Symbolization therefore implies understanding that the symbol is a token representing a referential class, in the context of a shared universe of meaning. This representational function is unique to symbolization, and is ultimately what distinguishes symbolic signs from non-symbolic signals.

Symbolic representation is not a property of an artifact or sign considered in isolation. It is a social and relational phenomenon, grounded in shared expectations about what the sign stands for and how it should be interpreted. We propose that a material or behavioral sign can be considered symbolic only if it satisfies the following conditions:

1. Representational intent—The sign is produced or deployed with the intention that its receivers will recognize both *that* it is a representation, and *what* it represents (Sinha 1988: 37).
2. Conventionality—The association between sign vehicle and meaning is socially learned and maintained.
3. Stability across contexts—Sign use is not *ad hoc* but recurrent and spatio-temporally distributed within a community.
4. Participation in a system—Individual signs gain meaning through relations with other symbolic signs and practices.

These criteria distinguish symbolic signs from purely functional artifacts, incidental markings, or individually motivated displays. They also differentiate symbolic representation from simple cue-based or affective communication found in non-human animals. These criteria should not be understood as a list of necessary and/or sufficient conditions for a decisive, saltatory evolutionary moment. Rather, symbolic attribution should be framed probabilistically and comparatively, emphasizing degrees of inferential support rather than categorical presence/absence. This framework underpins our assessment of the extent to which pigments, ornaments, engravings, figurative representations, and mortuary practices may be plausibly claimed, in context, to meet these conditions.

Because symbolic meaning is not directly observable, archaeological claims must rely on converging lines of evidence, including:

- Standardization and repetition
- Investment of labour beyond utilitarian necessity
- Contextual patterning (e.g., association with bodies, spaces, or structured deposition)

- Regional traditions and diachronic continuity.

If we accept the centrality of the representational function in defining symbolization, we have to accept that intentionally produced iconic representations, and visual signs with conventional meanings, are symbolic, although clearly not all visual signs can be considered either conventional or representational. Artifactual objects that are material bearers of meanings may not be evidence of symbolization, but they may nonetheless be evidence for the emergence of an early human *semiosphere entrenched in material signs*. In §3 we reviewed the lithic record of material culture, showing that innovations in tool manufacture and use were by no means limited to any one group of *Homo*. Moreover, we saw that comparable sophistication characterized developments in Africa and in Europe. In this section, we turn to objects that offer clues to the emergence of symbolization in the archaeological record from around 500 Ka through to 50 Ka or later, when the earliest cave paintings known to date were made. Specifically, we examine evidence for pigments, body ornamentation, mortuary practices, abstract drawings and engravings, and figurative representations. Such material signs have frequently been considered, with some caveats, as proxies for the emergence of symbolic cultures (Binford 1971; Carr 1995; d’Errico et al. 2003; Wreschner et al. 1980). As we shall see, the evidence suggests that the development or adoption of one of these practices does not invariably or rapidly pave the way for the emergence of the others. In fact, one practice may not lead to another for tens of millennia, suggesting that their asynchronous acquisition reflects instances of niche construction during which increasingly complex communication needs were accompanied by complexification of both embodied and exosomatic material signs.

Not all semiotic artifacts are representational, and non-representational semiotic artifacts appear in the archaeological record long before figurative representations. Our task is to use the different kinds of material signs to enable us to map the stages *en route* from signal to symbol. We make no attempt to speculatively interpret such signs in terms of their specific meanings. Our strategy, rather, is to treat non-representational material signs as visual *motifs* and *emblems*. A motif is “a vague or contentless (though not, by definition, formless) [design, pattern or structure] which, though it may serve an aesthetic or decorative purpose, does not seek to ‘stand for’ something outside itself [and] may be seen as visual equivalents of what, in language, Malinowski (1934: 316) called ‘phatic communion,’ which ‘serves to establish bonds of personal union between people brought together by the mere need of companionship and does not serve any purpose of communicating ideas’ (Sinha 1988: 41; see also Senft 2007).

If we regard a motif as a sign that is somehow aesthetically appealing or attractive (in the same way as a bower bird nest, but different in that the motif is intentionally produced by a maker *as a sign*), it can be unambiguously classified as a signal. However, once conventionalized, these physical patterns and structures may have served as affiliative markers of the maker’s membership, status, or owner-

ship. In so doing, they became *emblematic signs* which

“fall somewhere in between true representations and mere decorative or phatic motifs, since while they do not ... represent an object separate from themselves, they do permit, through design, the recognition, individuation and classification of the objects [including persons] which bear them” (Sinha 1988: 42).

In the next section, we describe and analyze in detail the non-technical artifacts (material signs) that are abundantly represented in the archaeological record, interrogating this record in order to trace the pathway, from motif, through emblematic sign, to representational symbol, that led from hominid proto-semiosphere to linguistically mediated human symbolic cultures.

Documenting this trajectory is challenging, especially in respect of practices for modifying the human body, which has long served as a medium upon which cultures have painted or inscribed their values, beliefs, and identities (Nowell and Cooke 2024). Whether through body painting, tattoos, piercings, scarification, fashion, or body modifications, these practices encapsulate traditions, mark significant life events, and differentiate groups within a society. Unfortunately, much of this cannot be derived from the archaeological record. While registering this caveat, we may note that many other constructive practices also left scant archaeological traces. The technology of weaving, for example, could have been employed in the making of slings for carrying children and baskets for carrying food and other goods, but its antiquity cannot be archaeologically established. As we shall see, semiotic practices and associated material signs appear at different times in Africa and Eurasia, and that some of them are not found in vast areas of Africa until a few thousand years ago. Moreover, some of these innovations seem to disappear for thousands of years and then reappear in other forms. Although the two appearances may in some cases be linked by continuous practices that left no intermediate traces, we suggest that they were in many other cases the result of independent (polycentric) cultural innovations and exaptations (d’Errico and Colagè 2018).

4.2. PIGMENTS

Mineral pigment use, in most cases of iron-rich rocks commonly called ochre, is seen among different hominins in Africa and Eurasia from as far back as 500 Ka. It is the only semiotic innovation that to a degree coincides with, or possibly even precedes, the beginning of the Middle Stone Age. Due to its known or inferred use in both semiotic practices and non-semiotic, utilitarian practices, ochre is often regarded as an ambiguous element in the archaeological record. Many scholars have argued that, without additional evidence, its presence alone cannot be taken as proof of semiotic use (Wadley 2005). Other researchers point out that in extant traditional societies, semiotic and utilitarian functions are often intertwined (Dapschaskas et al. 2022; d’Errico et al. 2010), suggesting that sustained, systematic use of pigments likely developed a semiotic dimension

relatively early. To resolve these contrasting views, several studies have focused on characterizing the behaviors associated with the use of mineral pigments, aiming to discern the complexity of these practices and assess whether they support semiotic interpretations. Evidence adduced to bolster the early semiotic use hypothesis includes the gradual increase in pigment use over time, a preference for specific colors, the sourcing of particular raw materials from distant locations, and the controlled heating of certain minerals to achieve desired hues. More compelling support for semiotic use includes the application of pigments to personal ornaments, the production of abstract engravings on ochre pieces and drawings with ochre crayons, and the preparation of small quantities of pigment better suited to semiotic than utilitarian purposes.

The discovery of red ochre fragments bearing modifications (scraping, grinding) to extract ochre powder dated to c. 305–320 KA at Olorgesailie, Kenya (Brooks et al. 2018) places this techno-practice at an earlier date than those reported for previous discoveries made at Kapthurin in Kenya, Twin Rivers in Zambia, and Wonderwerk, Canteen Kopje, and Kathu Pan 1 in South Africa (Barham 2002; Watts et al. 2016). The evidence for grinding may be relevant to body painting as a complement to the body ornamentation we discuss in §4.3. Examples of the Olorgesailie and later finds are shown in Figure 4.

Dapschaskas et al. (2022) identify three phases of ochre use in the African Middle Stone Age (500–320 Ka, 320–160 Ka, 160–40 Ka), each showing an increasing proportion of ochre at Middle Stone Age sites compared to lithics. The age of the oldest findings (320–280 Ka for Olorgesailie and even earlier for the southern Africa sites) suggests that the first users of red pigments probably possessed many archaic morphological attributes, notably in their brain shape (Neubauer et al. 2018). However, we observe for the African Middle Stone Age, the Middle Paleolithic in Eurasia, and in more recent periods, evolutionary trends suggesting a gradual and asynchronous complexification of practices involving the use of these materials. Ochre, relatively rare at African sites dated between 500 Ka and 160 Ka, becomes ubiquitous at later sites and can in some cases take the form of hundreds or even thousands of pieces bearing traces of modification in the form of facets due to abrasion against a grindstone and traces of scraping to produce ochre powder (Hodgskiss 2013; Rosso et al. 2017; Watts 2010). During this later period, a diversification of the geological sources of supply is observed, with the exploitation of sources of material of different qualities, and in some cases, the use of good quality sources located tens of kilometers from the sites (Dayet et al. 2016).

The use of mineral pigments of different colors and/or the preferential choice of certain hues is attested since the very beginning of ochre use, more than 300 Ka (Hodgskiss 2012; Rosso et al. 2017; Watts et al. 2016). At some sites ochre is heat-treated, and there are indications that this treatment was intentional and not the result of accidental heating in fireplaces as proposed by Wadley (2009). In the Levant, for example, ochre has been recovered from both

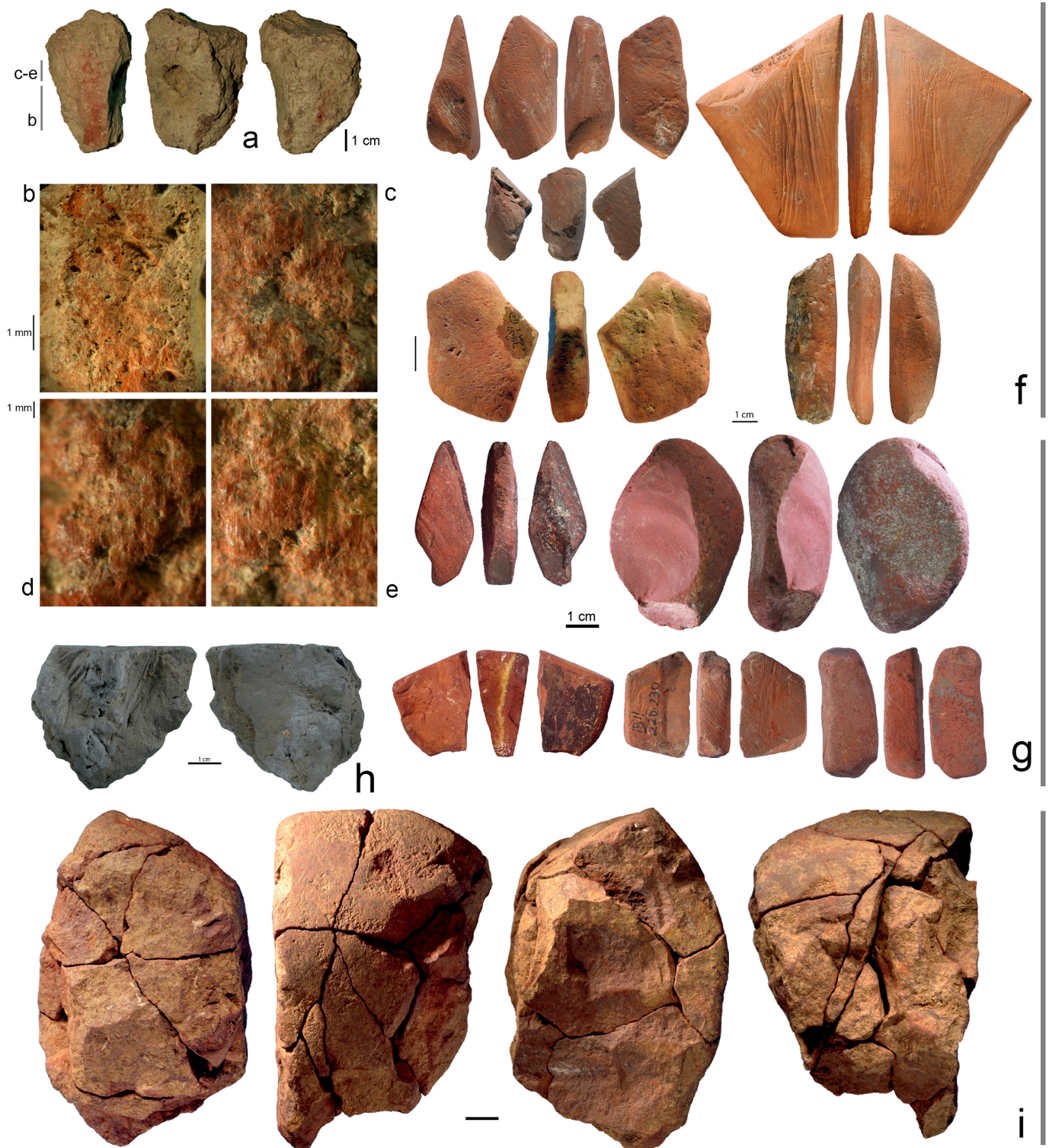


Figure 4. Pieces of ochre and manganese bearing traces of modification found at Middle Stone Age, Mousterian, and Châtelperronian sites. a) mineral pigment (dated to c. 280 Ka) in the Olorgesailie area, Kenya and (b-e) macrophotos showing traces of grinding; f) Klasies River, South Africa (c. 110–90 Ka); g) Porc Epic Cave, Ethiopia (c. 50 Ka); h) Pech de l'Azé, Dordogne, France (c. 50 Ka); i) Roc-de-Combe, Dordogne, France (c. 44 Ka) (photos a-f, h and i: F. d'Errico, g: modified after Rosso et al. 2023; scales=1 cm).

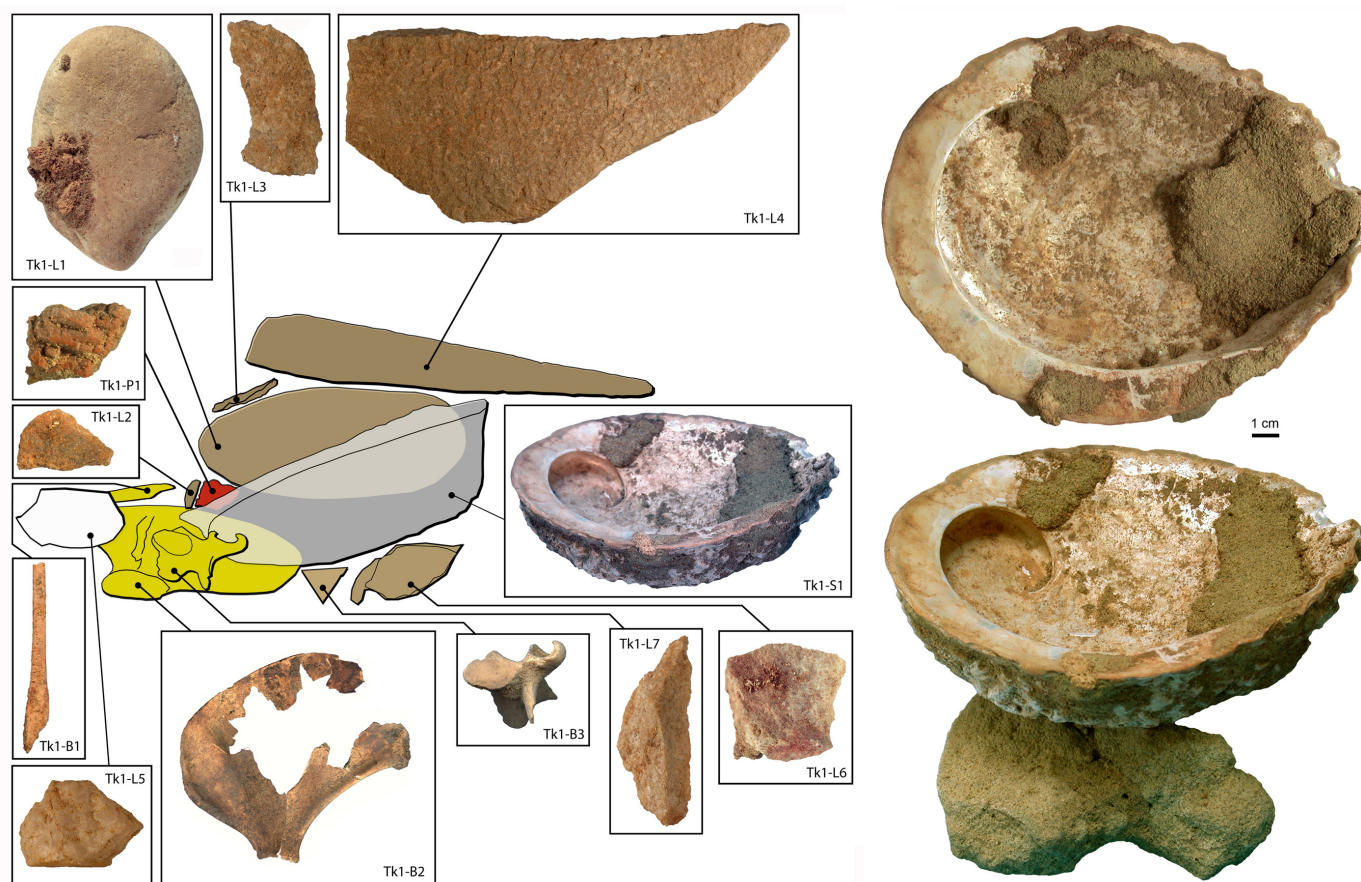


Figure 5. Tool kit for the production and storing of pigment compound found at Blombos Cave, South Africa, in 100 Ka layers. a) drawing with the location of objects composing the tool kit (Tk1-S1, abalone shell containing an ochred compound; Tk1-L1, quartzite pebble used to crush ochre; Tk1-L2 quartzite flake stained with ochre, Tk1-L3, quartzite blade stained with ochre; Tk1-L4, quartzite slab showing longitudinal streaks produced by abrading ochre pieces to produce ochre powder; Tk1-L5 and Tk1-L6, quartz flakes used to crush ochre; Tk1-L7, quartzite blade; Tk1-B1, limb bone, possibly used to apply ochre; Tk1-B2, seal scapula; Tk1-B3, seal vertebra; Tk1-P1, ochre fragment bearing traces of grinding; b) photos of the abalone shell with residues of pigment compound at its bottom (modified from Henshilwood et al. 2011).

Qafzeh and Skhul caves (120–90 Ka), where it was processed through grinding, scraping, and intentional heating to transform yellow goethite into red hematite (d'Errico et al. 2010; Hovers et al. 2003; Salomon et al. 2012). The association of ochre with burials and ornaments at Qafzeh strongly suggests semiotic intent (Bar-Yosef Mayer et al. 2009; Hovers et al. 2003). These findings indicate that Near Eastern populations engaged in pigment preparation and use in ways comparable to African MSA groups, highlighting the importance of the Levantine record for understanding the emergence of semiotic practices. Several archaeological sites show concentrations of ochre fragments and tools for producing red and yellow powder (Rosso et al. 2014). Finds of containers with paint residues (Figure 5), together with the tools to process them, reveal that 100,000 years ago pigment mixtures were made using several types of ochre by mixing them with other ingredients, probably in well-established proportions (Henshilwood et al. 2011).

The evidence for the use of pigments in early human

societies is extensive and varied. The consistent findings of ochre at numerous archaeological sites point to its importance in the daily and ritual lives of these ancient peoples. Beyond mere decoration, the strategic sourcing of high-quality pigments from distant locations indicates a complex network of trade and communication. Considering the diverse functions ochre served—ranging from body painting, which could signify group identity or status, to its use in burial practices and artistic expressions on cave walls—it is clear that ochre was a pivotal element in the semiotic practices of early humans. This multifaceted use underscores the sophistication of their social structures and the meanings they attached to various aspects of their environment. Such semiotic uses likely played a crucial role in the formation of early human societies, fostering group cohesion and communication. As we delve deeper into the archaeological record, we uncover layers of meaning that can shed light on the cognitive advances that paved the way for more advanced forms of signification and communication

in our evolutionary journey.

From c. 142 Ka onwards, ochre powder was used to change the appearance of shell beads (Sehasse et al. 2021).⁵ By 73,000 years ago ochre pencils were being used to produce schematic drawings (Henshilwood et al. 2018). From at least 40 Ka, ochre was systematically employed in funerary practices to cover the body and attires of the deceased, applied to cave walls to produce figurative representations, and to ornaments, clothes, and skin covering the floors of habitations. The evidence for pigment use in Eurasia before the arrival of *H. sapiens* (Hoffmann et al. 2018a; b; c; Jaubert et al. 2016; Joordens et al. 2015; Majkić et al. 2018; 2017; Peresani et al. 2013; Villa and Roebroeks 2014; Zilhão et al. 2007; 2010; see Roebroeks and Soressi 2016 for a synthetic view) clearly indicates that it was not exclusive to African (MSA) populations. Neanderthal and *H. heidelbergensis* engagement in such practices starting from 400 Ka is supported by finds of pigments and pigment-processing tools (Bodu et al. 2014; de Lumley et al. 2016; Pitarch-Martí et al. 2018; 2019; Roebroeks et al. 2012). *Homo heidelbergensis*, the ancestor of the Neanderthals, used red ochre at c. 400 Ka at Terra Amata, a site near Nice in France. The use of red and especially black pigments became a widespread practice among Neanderthals after 60 Ka, as evidenced by tools used to process mineral fragments rich in iron oxides, manganese oxides, and graphitic siltstone found in many European sites during this period (Bonjean et al. 2015; Dayet et al. 2014; Pitarch-Martí et al. 2019; Salomon et al. 2016; Soressi et al. 2008). The traces of modification recorded on the mineral pigments do not substantially differ from those observed at contemporaneous African sites.

The evidence presented above demonstrates that lumps of ochre were ground to produce pigment powder by at least 280 Ka, that tool kits were developed to create pigmental compounds composed of different ochre types and other ingredients by at least 100 Ka, with iron-oxide rich rocks being deliberately heated to change their color, that types of ochre of particular shades and properties, only available dozens of kilometers far from the main habitation site, were systematically searched for or acquired through exchange with neighboring groups. We also saw that ochre pieces were, by at least 70 Ka, shaped into “pencils” for drawing abstract patterns on stone, and that pieces of ochre have been found that have been engraved with abstract patterns. We observe that similar abstract patterns engraved on ochre are repeatedly found at a number of sites located in the same region, as recorded in the MSA of southern Africa, and that ochre was used to change the color of shell beads. All the above behaviors are attested at sites older than 50–40 Ka.

A recurrent argument seeking to discount or downplay semiotic uses of ochre, engravings, or beads is that they would have served an aesthetic rather than semiotic function. However, we have no reason to exclude the aesthetic properties of motifs from the broad category of semiotic uses that were prior to symbolic uses *sensu stricto*. Implicit in this argument is the assumption that “aesthetic” equates to individual taste or personal preference. If pre-

historic hominins were primarily motivated by individual taste, we would expect, at a group level, a high degree of variability in practices, reflecting individual shifts in preferences. However, archaeological evidence shows the opposite—there is a remarkable consistency in materials, techniques, and practices across vast stretches of time and space at the same sites and evidence that when changes occur in the mineral pigment preference and processing (Dayet et al. 2019) they coincide with marked changes in lithic technology, indicating mineral pigment use was an inherent component of distinct cultural traditions rather than an idiosyncratic behavior of a single individual. An aesthetic shared by members of a group likely required more than passive imitation; it depended on forms of communication capable of stabilizing and transmitting stylistic norms across individuals and generations. While it is true that fashion trends can spread rapidly through processes of implicit diffusion without explicit complex communication, such trends tend to be volatile and short-lived. By contrast, the archaeological evidence we discuss—for example, consistent pigment use within sites and regions—points to durable, socially maintained conventions. The persistence of such shared aesthetics therefore implies not just copying but coordinated communicative practices, including negotiation, reinforcement, and teaching, all of which presuppose high levels of communicative coordination.

A different methodological objection is that ochre was used only for practical purposes. However, it is common in historically known human societies to use mineral pigments both for practical purposes (e.g., protection against insects and ultraviolet radiations) and semiotically (for body, cloth, objects, and wall painting). In none of these societies is pigment powder exclusively employed for practical uses, the semiotic dimension being always present, even if at different degrees, according to the examined cultural setting. Maintaining a double standard in the interpretation of the archaeological ochre record, accepting the semiotic dimension for the use of ochre in historical human societies but denying it in chronologically distant ones, is hardly justifiable, especially given that the practices described above do not appear abruptly in the archaeological record. Ochre use becomes gradually more prominent and complex, but is also absent in some regions or periods. This suggests a process during which mineral pigments, in some contexts and not in others, gradually took on an increasing role in society and were used in more diverse ways and for different practical and semiotic functions.

While some hominin groups probably used ochre for body painting and certainly for shell decoration, engravings, drawing, or for enhancing engravings on bone by adding ochre in the incised lines, others engaged in only some of these practices, or did not use ochre at all. This cultural variability implies a learned, culturally transmitted behavior, reflecting choices specific to different social contexts, beliefs, and traditions within distinct groups.

The same argument and evidence applies to early personal ornament use. For example, particular shell species were repeatedly selected for bead making over millennia,

between 140 Ka and 70 Ka, in North and South Africa, despite the availability of numerous other shell species that may have been used for the same purpose. Additionally, consistencies in the way beads were strung and the complex technology used to alter bead color through heating in reductive environments show a complex, stable tradition, not a series of individual aesthetic choices. The enduring nature of these practices suggests that they were tied to identity, group affiliation, or status. Such patterns indicate that these practices were at least transitioning to emblematic rather than solely aesthetic, motif-like uses, with the form and materials conveying shared meanings rather than transient preferences. As to the nature of such shared meanings, these are difficult to establish, but one hypothesis that has been advanced is that the evolution of ochre use is related to increasingly complex practices involving “blood symbolism” (Watts 2024). The Female Cosmetic Coalitions Hypothesis (Power et al. 2024) proposes that early human females formed alliances to collectively resist male dominance and coercion, thereby gaining social control and influence over reproductive decisions. These female coalitions are seen as pivotal in shaping human cooperation, social norms, and cultural practices. The use of ochre served (from perhaps c. 500–380 Ka) as a medium that reinforced social bonds and communicated coalition membership, consistently with the account advanced by Hrdy (2009) on the evolution of co-operative childcare. Although the proto-symbolic use of ochre between 500 Ka and 160 Ka is uncertain, after 160 Ka it becomes clear and unambiguous. Watts (2024) suggests that this was associated with collective rituals centered on what he calls “shared fictions.” We prefer to designate, following Castoriadis (1987), the extension of symbolic practices to new “irrealis” ontologies as indicating the emergent social imaginary that structures both belief systems and social relations. As we shall see below, the use of ochre to change the color of shell beads is attested starting from 140 Ka.

While the evidence clearly suggests, then, that early uses of ochre included semiotic practices, we should still be cautious in assuming these practices were identical in nature, significance, and linguistic situatedness as those seen in historically known societies. Key distinctions likely lie in the rate of cultural turnover, as early proto-symbolic systems appear to evolve gradually, with probable long-term persistence in the meanings associated with symbolic material culture. This slower cultural evolution likely reflects the constraints of emerging cognitive and communicative systems, which might have limited hominins’ capacity for semiotic innovation. Unlike the rapid, dynamic re-interpretation of symbols typical of many recent societies—facilitated by sophisticated linguistic and communicative capabilities—the slow evolution of these early practices suggests that early hominin groups employed communication systems that were less elaborate than the EMLs that facilitate rapid, cumulative cultural innovation. Moreover, shifts in ochre use, ornamentation, and other semiotic practices are often regionally specific, at times vanishing from certain areas entirely, pointing to an early cultural landscape with

limited exchange and diffusion of practices across groups. This pattern suggests that communication networks among these early societies may have been more localized, with less emphasis on widespread cultural integration or sharing of semiotic practices. Consequently, sign systems of different complexity could have evolved independently, reflecting isolated innovations rather than trends propelled by broad, cross-group communication. This regionalism contrasts with the interconnected cultural landscapes of later societies, where innovations spread more rapidly and extensively.

4.3. BODY ORNAMENTATION

Body painting, scarification, tattoos, dental filing, skeletal deformations, mutilation, hairstyles, elaborate clothing, and ornaments are among the technologies created by human populations to transform the physical body into a carrier of material signs bearing shared meanings for the members of the group to which the individual belongs, and potentially for other groups with which the individual comes into contact (Manni and d’Errico 2023). Many of these technologies, however, have left no detectable trace in the archaeological record or, in the case of pigments, only circumstantial evidence. Personal ornaments made of non-perishable materials are, in contrast, a privileged indicator for tracing back the emergence and the complexification of techniques to culturally transfigure the body. Numerous anthropologists (Barth 1969; Heizer 1978; Hodder 1977; Kinnietz 1972; Trigger 1978) have observed that objects of personal decoration play a crucial role in the self-identification of ethnic groups. Ornaments may strengthen the sense of belonging to the group and increase its cohesion, though this is not their only role, and does not preclude ornaments and other forms of body modification from having an aesthetic dimension. They can also establish boundaries between neighboring groups by becoming a tangible proxy of linguistic, ethnic, and religious affiliations. Within a society, personal ornaments often serve to mark an individual’s membership of one or more social groups or a personal status (Brain 1979; Carey 1998; Cordwell and Schwarz 1979; Dubin 1987; Kuper 1973; Morris and Preston-Whyte 1994; Roach and Eicher 1965; Sciamia and Eicher 1998; Strathern 1971; Turner 1980). In other words, such objects may be markers of group affiliation or status within the group.

Discoveries over the last 20 years (Figure 6) reveal, just as for pigments, an ancient origin for ornaments, contradicting the hypothesis that ornamental objects were invented and first used by modern humans when they arrived in Europe c. 42 Ka. Sporadic occurrences were followed by the invention of specific techniques and a gradual evolution leading to shared ornamental codes. The earliest known personal ornaments are found in Africa. They consist of shells of perforated marine gastropods of the species *Tritia gibbosula*, covered with ochre. These were found at sites in Morocco and Algeria dating back to between 142 Ka and 80 Ka (Bouzouggar et al. 2007; d’Errico et al. 2009; Schasseh et al. 2021; Steele et al. 2019). Perforated and unperforated shells belonging to the same species and bivalves of the

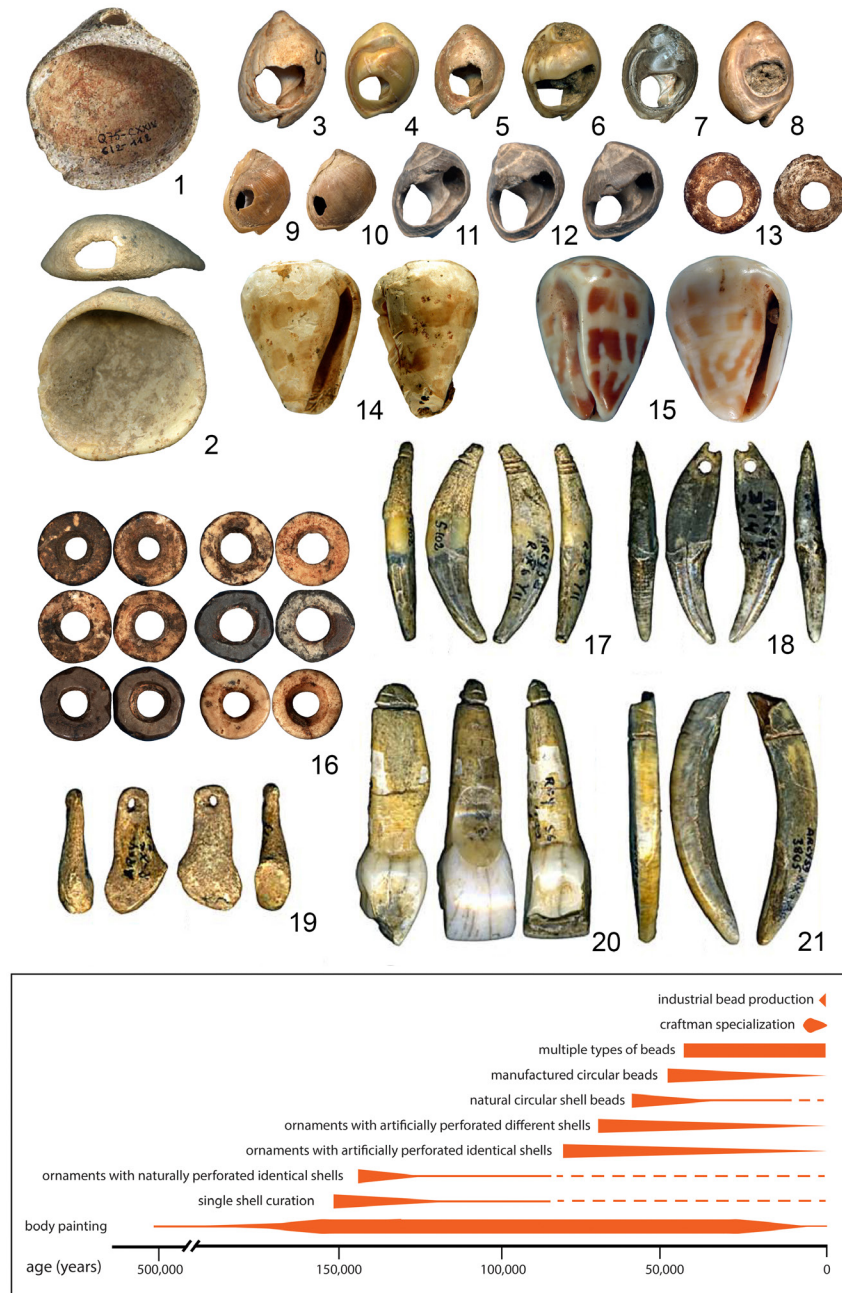


Figure 6. Top: Earliest instances of personal ornaments: 1) *Glycimeris* shell with traces of red pigment and a natural perforation, Qafzeh, Israel, c. 95 Ka; 2) *Glycimeris insubrica* shell with a natural perforation, Cueva de Los Aviones, Spain, c. 115 Ka; 3) *Tritia gibbosula* shell with a natural perforation, Skhul, Israel, c. 115 Ka; 4–5) Grotte de Pigeons, Taforalt, Morocco, c. 80 Ka; 6): *Tritia gibbosula* shell with a natural perforation, Rhafas, Morocco, c. 80 Ka; 7) *Tritia gibbosula* shell with a natural perforation, Ifri N'Amman, Morocco, c. 120 Ka. Note the dark coloring of the shell most likely due to heating; 8) *Tritia gibbosula* shell with a natural perforation, Oued Djebbana, Algeria; 9–12) *Nassarius kraussianus* shells, Blombos Cave, South Africa, c. 73 Ka, artificially perforated. Note the difference in perforation size and type between shell beads 9–10 and 11–12. The dark coloring of the latter is due to heating; 13) naturally perforated *Conus* apexes used as beads, Panga ya Saidi, Kenya, c. 60–40 Ka; (14) *Conus ebraeus* shell bead associated with the burial of an infant, Border Cave, KwaZulu-Natal, South Africa, c. 74 Ka; 15) *Conus ebraeus* shell bead, Border Cave, KwaZulu-Natal, South Africa, c. 74 Ka; 16) ostrich eggshell beads, Panga ya Saidi, Kenya, c. 33 Ka; 17–21) personal ornaments made by Châtelperronian Neanderthals at the Grotte du Renne, Arcy-sur-Cure, Yonne, France, c. 45–42 Ka. Bottom: Multistep evolutionary scenario for the culturalization of the human body based on available archaeological evidence (modified from d'Errico 2025 and d'Errico et al. 2023).

genus *Glycimeris*, found respectively at Qafzeh and Skhul, Near East, date back to about 110 Ka (Bar-Yosef Mayer et al. 2009; 2020). Several species used as beads are found at Sibudu, Kwa-Zulu Natal, in layers predating 70 Ka (Vanhaeren et al. 2019). Perforated and ochred marine gastropods, belonging to the species *Nassarius kraussianus*, are used as ornaments at Blombos Cave, Western Cape, around 73 Ka (d'Errico et al. 2005).

Use wear analysis, chemical analysis, and experimental replication of Blombos Cave beads identified a change through time in the way beads were strung to produce necklaces and bracelets, as well as the probable employment of heating techniques to blacken the shells (d'Errico et al. 2014; Vanhaeren et al. 2013). At Border Cave, Kwa-Zulu Natal, a whole *Conus ebraeus*, perforated and ochred, was found in a pit dated to 74 Ka, in which the body of an infant was deposited (d'Errico and Backwell 2016). Ornamental practices using marine shells appear to have ceased or greatly diminished from 70 Ka. Ornamental objects that took over from about 50 Ka in some parts of Africa and later in others consisted of circular ostrich eggshell beads. Technological and morphometric analysis of this beadwork identifies long-term trends suggesting a gradual specialization of manufacturing techniques associated with regionalization and the creation of exchange networks (d'Errico et al. 2020; Miller and Wang 2021).

A recent synthesis (d'Errico et al. 2023) identifies at least ten stages in the evolution of body modification and ornamentation practices (see Figure 6). The first stage, observed in Southern and East Africa, and in Europe, would correspond to the use of ochre for body decoration. A subsequent phase, starting 150–100 Ka, observed primarily in southern Africa and sites in western Asia and Europe, involved the collection and curation of marine shells without modification. Some of these shells present natural perforations and may have been used as ornaments or amulets. This phase was followed by another, starting 140 Ka, where shells with natural or anthropogenically modified perforations were utilized as adornments. During this period, there is evidence suggesting the covering of pendants with ochre, whether intentional or accidental due to contact with ochred skin. The limitation to natural perforations restricted the variation in shell arrangements. This practice correlated with specific heating techniques to modify shell colors. During the following phase, advances in perforation techniques allowed for varied arrangements of homologous ornaments. Sites like Sibudu rock shelter and Blombos Cave demonstrate this evolution, occurring around 80 Ka to 72 Ka. Subsequent developments involved integrating larger shells into ornamental items predominantly made of smaller shells. This integration is recorded at sites like Blombos Cave and Sibudu around 80–70 Ka. Ornaments used by Neanderthals in Europe also fall within this phase. Evidence includes the collection, coloring, and possible use as pendants of marine shells (Peresani et al. 2013; Zilhão et al. 2010); use of feathers and raptor talons for ornamental purposes (Finlayson et al. 2012; Fiore et al. 2016; Peresani et al. 2011; Radović et al. 2020; 2015; Romandini et al. 2014)

and the collection of exotic items (Moncel et al. 2012; Soressi and d'Errico 2007).

Turning our attention back to Africa, the following phase involved the use of fragments of *Conus* shells heavily modified and perforated by natural agents as ornaments. This stage is so far only known from Panga Ya Saidi, Kenya, where, in layers dated between 60 Ka and 45 Ka, circular, naturally perforated *Conus* spires were used as beads. This use opened the way to the following, seventh step—the production of fully manufactured circular beads made from ostrich eggshells and, more rarely, stone, possibly starting around 50 Ka in East Africa. The eighth evolutionary stage, beginning around 45 Ka, marks a significant diversification in personal ornaments across Eurasia, featuring a wide array of raw materials, shapes, production techniques, and attachment methods. This variety rivals the richness seen in later prehistoric and historic ornament traditions, likely reflecting the use of ornamentation to mark ethnic affiliation and group identity (Baker et al. 2024; Vanhaeren and d'Errico 2006). The personal ornaments made by Châtelperronian Neanderthals at the Grotte du Renne, Arcy-sur-Cure, Yonne, France, c. 45–42 Ka (see Figure 6) fall within this phase. The presence of exotic items from long-distance trade and their selective inclusion in Upper Paleolithic burials between c. 34 Ka and 10 Ka suggests that these ornaments may also have been indicators of social inequality. The ninth stage introduced ornament production by specialized artisans, with items crafted for members of different social groups, reflecting increasing social complexity and the rise of production economies from the Neolithic onwards. Finally, the tenth stage, from the 18th and 19th centuries, corresponds to the industrial production of ornaments, making adornments widely accessible across societies. This stage democratized access to ornaments, including beads made from synthetic gemstones, pearls, and amber, which previously held special value due to rarity or specialized craftsmanship.

This step-by-step progression displays a shift from natural objects to artificial geometric shapes and standardized colors, signaling a trend toward the “artificialization” of body ornaments. The complexity observed in ornaments and ochre use likely parallels developments in other body culturalization practices, which similarly required advanced techniques, social semiotic codes, and specialized roles for continuity. This gradual process began with simple body adornments and evolved into sophisticated practices involving rare or exotic materials and specialized artisans. Over time, these technologies created complex visual codes, diversified the social roles of ornaments, and transformed them into valuable, inheritable goods. The neuro-cognitive adaptations required to interpret these intricate symbols facilitated a deeper understanding of identity and social status, as well as the quantification of wealth displayed on the body (Salagnon et al. 2024). These processes, reliant on novel communication and cultural transmission strategies, bestowed new values upon these objects, permitting the construction of symbolic niches in which the ornamented human body serves as a platform

for self-expression and differentiated identity construction. In sum, the evolution of body modification technologies reflects the polycentric expansion of the human niche and a need for increasingly complex symbolic communication that must have required, to be transmitted, a gradual complexification in other, including linguistic, modes of communication.

4.4. MORTUARY AND FUNERARY PRACTICES

Many animal species exhibit behaviors that separate areas for urination and defecation from spaces for eating, resting, or breeding, which can be seen as an elementary, quasi-normative embodied niche differentiation. Some of these behaviors extend to what we might consider mortuary practices, involving the placement or handling of deceased members of the group. However, at Sima de los Huesos, the deliberate placement of bodies deep within a cave alongside an Acheulean handaxe crafted from exotic lithic material suggests a practice closer to what we define as funerary rather than purely mortuary. Their association with a single biface shaped in an exotic lithic material—a carefully crafted artifact transported over long distances—suggests that the deposition was not merely pragmatic but involved the deliberate placement of a culturally valued object. The exotic provenance of the material indicates that the biface carried symbolic or social significance, which may have been central to the meaning of the deposition. The concept of funerary practices involves more than the practical disposal of bodies; it implies the ritual making of a transition from a living person to a symbolically significant other (Pettitt and Anderson 2020). This distinction has implications for understanding the development of symbolism in human evolution. Funerary practices, unlike simple mortuary actions, suggest that the body of the deceased becomes a symbolically-invested object within the social system and semiosphere of the group.

Although the archaeological record limits our ability to determine the specific meanings early humans attached to such practices, evidence from more recent societies highlights that funerary rituals often rely on complex symbol systems to convey the meaning of the deceased within a broader cultural context. For example, in ancient Egypt, the mummification of pharaohs, their placement in elaborately decorated coffins, and entombment within monumental structures signify the pharaoh's transition from earthly life to a divine, eternal existence.

Trevor Watkins (2024) suggests that in the Epipaleolithic-Neolithic period of Southwest Asia, the burial of select individuals under the floors of buildings did not necessarily indicate a belief in an afterlife. Instead, these burials marked the settlement itself, with the bodies signifying group affiliation and laying claim to a particular place; in this account, the deceased's individual identity is subsumed in its indexing of the continuity and identity of the group. However, burial inside the house with a clear symbolic dimension is found in existing societies:

“For the Amondawa [an Amazonian ethnolinguistic group], the house is not only a place to live, it is also a body that has life. Traditionally, the Amondawa house protected not only the living, but also the souls of the dead, who were buried beneath the fires that warmed each nuclear family. Inside the house, the birth of new life was celebrated and the dead were mourned, keeping their souls in the house so that they would not become lost spirits or hauntings” (Sampaio et al. 2020: 191).

Both the remains of the deceased and the house are beings with potential agency and animacy in the grammatically expressed social imaginary of the Amondawa. In many more familiar contexts, such as military funerals, ritual practices go beyond honoring the individual alone. They embed the memory of the individual within a framework of collective values—nationality, valor, sacrifice—reinforcing the social and semiotic connections that bind the individual to the community. In a broader sense, we can see rituals, including funerary practices, as structured behaviors that declare and reinforce the status of individuals or groups within a shared symbolically organized social imaginary. Rituals surrounding birth, initiation, marriage, and death each mark significant transitions, involving not only specific patterns of behavior but also symbolic objects reserved exclusively for these ceremonial purposes. Other rituals, such as regular religious services, do not signify a transition but serve to reaffirm an individual's status within the community.

Evidence for the evolution of funerary practices is inevitably biased by preservation factors, since some symbolic funerary practices that involved exposure to the elements, destruction, or consumption of the deceased body would leave little, if any, trace (Zilhão 2005). However, archaeological evidence shows a gradual evolution and diversification of these practices, with primary burials only emerging around 120 Ka, regardless of the fossil species involved. This trend suggests that funerary practices reflect the continuous expansion of human niches, progressively encompassing both visible and invisible transcendental spaces and more complex rituals to communicate and perpetuate, according to the human culture examined, the memory of the deceased and/or the place dedicated to the dead.

In the past, paleoanthropologists viewed the invention of primary burials—where a pit was dug to place the deceased and then covered with sediment—as a critical transition, symbolizing the shift from a humanity without semiotic practices attached to death to one that engaged in them. Neanderthal evidence for primary burials was often met with skepticism, as many such finds had been excavated long ago, leading to concerns over their reliability. This situation reinforced a narrative that emphasized a sharp divide—Upper Paleolithic burials were seen as a cohesive phenomenon marking a “symbolic revolution,” while earlier, sporadic instances were regarded as limited precursors to symbolic thought. This interpretive framework no longer holds. Hominins whom archaeologists would not

until recently have thought capable of care for the dead deposited, over a period of several hundred thousand years, the bodies of deceased group members in the bottom of caves or in natural crevices, or removed the soft parts of their mortal remains for preservation and handling (Pettitt 2010; Stiner 2017). Recent studies show that these practices have a long evolutionary history and may go back to our common ancestor with the chimpanzees (Pettitt and Anderson 2020). Chimpanzees have been observed to show attention and care toward deceased group members, such as by grooming or gently touching the bodies, guarding them, or even carrying dead infants for extended periods (Anderson 2018; Van Leeuwen et al. 2016; 2017; 2018). These behaviors suggest an awareness of death and perhaps an emotional response to it, which aligns with the definition of mortuary practices as behaviors related to the treatment of the dead, to be distinguished from funerary practices, describing activities relating to the disposal of the dead and to their subsequent commemoration.

Burials and other funerary practices can be considered proto-symbolic because they reflect intentional actions taken by the living to manage and honor the dead, often beyond practical needs. These acts—such as positioning bodies, adding grave goods, or carefully selecting resting places—go beyond awareness of death, perhaps implying a concept of an afterlife or spiritual presence (Rappaport 1999). By engaging in these rituals, which were constitutive parts of the social imaginary, early humans expressed values, beliefs, and emotions about life, death, and community. Such practices construct and depend upon material representations of complex conceptual systems in the physical treatment of bodies. A challenge for evolutionary thanatology is to elucidate how and when practices linked to morbidity, i.e., the examination of corpses and their associated emotions, became culturally transmitted ritual practices with symbolic meanings. Pettitt (2018) argues that since the means to achieve this, such as song, storytelling, wearing mourning garments, and so on are archaeologically invisible, the transition to funerary practices must be inferred from the identification of places in which the deliberate segregation of the dead from the living has been performed. Variations in treatment based on age or gender, the identification of primary or secondary burials as well as the systematic retention, or deliberate deposition or alteration, of body parts may signal this key transition. The archaeological records indicate that this transition was probably very long in duration, and practices varied markedly from one region to the other.

Sima de los Huesos, located in the Atapuerca Mountains of Spain, contains the largest collection of Middle Pleistocene hominin fossils, dated to c. 430 Ka, including the remains of at least 28 individuals. The concentration and arrangement of these remains, deep within the cave system, and their association with a single biface shaped in an exotic lithic material, imply intentional placement of bodies in a remote and difficult-to-access location. Possible evidence of a similar practice comes from Africa, where remains of a small-brained hominin, *Homo naledi*, were found

deep within the Rising Star cave system, dated to between 335 and 226 Ka (Dirks et al. 2017; Hawks et al. 2017). The excavators suggest that *H. naledi* may have engaged in burial practices, though as critics have pointed out the evidence is limited (Foecke et al. 2025; Martín-Torres et al. 2024). Even if the accumulations of *H. naledi* remains represent funerary caching (intentional deposition of the dead) rather than formal burial, the implications are nonetheless profound. While lacking the elaboration of later mortuary practices, such behavior would still constitute an important threshold in extending socio-emotional concern beyond the life of the individual, and would suggest that elements of funerary practice predate *Homo sapiens*.

Middle Paleolithic sequences at Qafzeh and Skhul caves (Israel) provide some of the earliest well-accepted primary burials of *Homo sapiens*. At Qafzeh, the possible association of human burials with ochre-stained ornaments demonstrates semiotic practices linked to body modification and mortuary treatment (Bar-Yosef Mayer et al. 2020; 2019; Tillet 1999; Vandermeersch 1981). These finds strongly suggest a symbolic dimension, situating these records among the foundational milestones of mortuary practice worldwide. The recently excavated Tinsmet Cave (Israel, ca. 110–100 Ka) provides exceptional evidence of intentional burial practices, at least five human burials—two complete skeletons and three skulls—carefully placed in fetal positions within pits and accompanied by ochre fragments, some from distant sources. The exceptional preservation of ash-cemented deposits even preserves interlaced fingers, providing compelling evidence for early symbolic and ritual burial behavior shared among *Homo sapiens* and Neanderthal-like individuals in the Levant (Zaidner et al. 2025).

The funerary practices of Neanderthals have been debated for over a century, largely because most evidence predates modern analysis methods. Recent discoveries and reassessments of old data have shown that Neanderthals treated the deceased differently depending on the period and region, with practices including cannibalism, secondary burials, curation of selected remains, and primary burials (Maureille 2022; Pettitt 2011, 2002). The earliest known primary burial is that of Tabun C1, a probable Neanderthal with archaic features, dating to around 120 Ka and possibly 190 Ka (Richard et al. 2024). A recent study (Jaubert et al. 2022) identifies 44 Neanderthal primary burials across 23 sites. Most sites have a single burial. Two sites, La Ferrassie and Shanidar, feature five to seven burials. Neanderthals buried group members regardless of age and sex, including newborns, with a notable lack of adolescents and young adults. Offerings, such as stone tools, stones with cupules, and faunal remains, are present in several cases, though this is still debated. This range of practices suggests the presence of different and evolving mortuary traditions, likely reflecting varied symbolic systems and shifting social or cultural frameworks within Neanderthal groups over time (Pomeroy et al. 2020).

Compared to these practices, primary burials, i.e., burying a body in a deliberately dug grave, appear to be relatively recent in Africa. Until recently, only two truly an-

cient burials, Taramsa in Egypt and Border Cave in South Africa, dated respectively to 68 Ka and 74 Ka, were known. The former could be just a funerary caching, i.e. the intentional placement of a deceased individual's body in a hidden location without formal burial of the body in an excavated pit. Although information on the second, discovered in 1941 and dated to c. 74 Ka, is limited, reappraisal of the evidence supports the burial of an infant in a pit with a perforated *Conus* shell covered with red ochre (d'Errico and Backwell 2016). The earliest known African burial, dated to approximately 78 Ka, is that of a 3-year old child, found recently at Panga ya Saidi, Kenya (Martín-Torres et al. 2021). The body was deposited and buried in an excavated pit. No ochre or grave goods were put close to the child's body, but analysis of sediments and the arrangement of the bones shows that the body had been protected by being wrapped in a shroud and that the head had likely rested on an object of perishable material—a practice only attested with certainty from 40 Ka at Mungo, Australia, and after 34 Ka in Europe, at Sungir, Russia, and Paviland, Wales.

Upper Paleolithic burials in Europe are marked by significant variability and discontinuities, both chronologically and geographically. No reliable burials are associated with the Proto-Aurignacian and Aurignacian (42–34 Ka). Over 60, single and multiple, burials have been documented in the Gravettian (34–24 Ka). Geographical variation in grave goods and signs of ritual treatment suggest a growing emphasis on social identity and symbolic behavior within Gravettian groups (Baker et al. 2024; d'Errico and Vanhaeren 2006) while, at the same time, identifying evidence for social stratification and a reduced proportion of infants, interpreted as evidence for infants not being considered as independent persons (and, hence, worthy of burial at their death) but only becoming so after weaning (Zilhão 2005; but see Nowell 2020). Primary burials become rare between 20 Ka and 15 Ka to acquire again importance during the Magdalenian in France, Spain, and Central Europe, and the Epigravettian in Italy and the Balkans. However, primary burials coexist during this period with cannibalism and other funerary practices, further supporting polycentrism rather than a straightforward evolution from simple to more complex mortuary practices (Marsh and Bello 2023).

4.5. ABSTRACT ENGRAVINGS, DRAWINGS, PAINTINGS

As we have already noted for symbols and icons, deliberately made abstract, non-figurative designs are not found in any non-human primate species in the wild. The earliest human-made designs, found in Africa and Eurasia at sites dated to between 450 Ka and 40 Ka include engravings, drawings, paintings, finger flutings, hand stencils, and possibly carvings (see d'Errico and Nowell 2000 for a possible example of the latter). They are associated with a number of fossil human species including *Homo erectus*, *Homo ergaster*, Neanderthals, and early *Homo sapiens*, becoming very common in some *H. sapiens* populations after 45 Ka. The interpretation of the earliest engravings, found at sites older than 45 Ka, remains controversial on account of their rela-



Figure 7. Zig-zag pattern engraved on a fresh water bivalve belonging to the genus *Pseudodon* found at Trinil, Java, in layers dated to c. 500 Ka (photo and drawing modified after Joordens et al. 2015). Shell length about 9cm.

tively small number and, according to some authors, the lack of features allowing them to be visually discriminated as signs forming part of a coded system.

The earliest known abstract engravings are incised on stone, bone and shells (Crémesdes et al. 1995; Joordens et al. 2015; Majkić et al. 2018; Peresani et al. 2014); the earliest known example being a zig-zag pattern incised on a fresh water shell from the *Homo erectus* site of Trinil (Figure 7), Java, dated to c. 540–430 Ka (Joordens et al. 2015).

Bone, ivory and antler objects bearing multiple incisions, interpreted as deliberate engravings, are reported from more than forty sites from Europe, the Near East, and China dated to the Lower (3 Ma to 300 Ka) and Middle Paleolithic (300–40 Ka) (e.g., Langley et al. 2008; Li et al. 2019; Majkić et al. 2018).⁶ Although a number of these incisions have been reinterpreted as the consequence of natural phenomena (d'Errico and Villa 1997), and others await detailed analysis, a substantial number have been analyzed and shown to be human-made and difficult to interpret as resulting from subsistence activities (d'Errico et al. 2018; Leder et al. 2021; Majkić et al. 2017; Zilhão 2014). The oldest of these are bone fragments bearing engraved lines (Figure 8), at the Lower Paleolithic site of Bilzingsleben, Germany, dated to c. 350 Ka (Bednarik 2024).

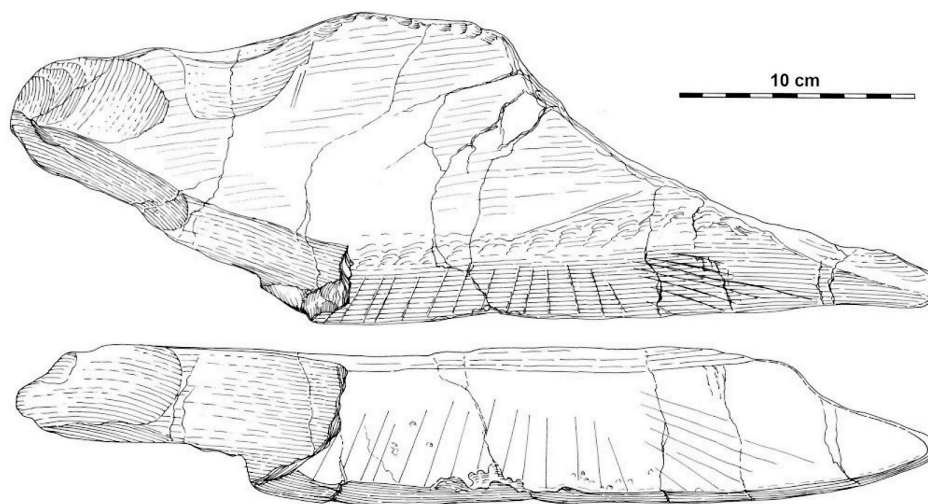


Figure 8. Mammoth bone fragment found at the site of Bilzingsleben, Germany, dated to c. 350 Ka, bearing two groups of subparallel engraved lines (after Mania and Mania 1988).

Recent European discoveries further challenge earlier accounts in which semiotic practices in deep caves (that may have been ritual performances) were held to be an innovation introduced by “modern” humans. At Bruniquel Cave, Tarn-et-Garonne, France (Jaubert et al. 2016) Neanderthals broke four tons of stalagmites 176 Ka, in an area hundreds of meters from the entrance, arranging the fragments to create two large subcircular structures on the cave floor (admittedly this is an abstract structure rather than an abstract drawing or engraving). Recent 3D surface analyses of incised artifacts from the Levantine Middle Paleolithic strengthen the case for early intentional non-utilitarian engravings. At Manot Cave, a Levallois core dated to ca. 55 Ka bears 64 convergent incisions forming a radiating fan pattern, clearly predating the final knapping stage (Goder-Goldberger et al. 2025; Marder et al. 2018). Similar geometric traits are observed on the engraved Levallois core from Qafzeh (~100 Ka) and the flint plaquette from Quneitra (54 Ka), where semi-circular arcs and parallel lines indicate deliberate design (Hovers et al. 1997; Shaham et al. 2019). In contrast, two incised pieces from Amud Cave (68–55 Ka) show shallow, irregular marks best explained as by-products of use as abraders. The comparative study thus places the Manot, Qafzeh, and Quneitra engravings in a coherent group of intentional semiotic, possibly aesthetic, practices, distinguishing them from incidental modifications such as those at Amud. Although these finds remain rare and isolated in time and space, they demonstrate that Levantine Middle Paleolithic groups occasionally engaged in the creation of abstract patterns beyond utilitarian needs. Similar engravings are found at Middle and Early Upper Paleolithic sites in Europe (Majkić et al. 2018) and China (Li et al. 2019; Peng et al. 2012).

Uranium-thorium (U-Th) dates on carbonate crusts overlaying paintings provide minimum ages of 64.8 Ka for finds in three Iberian caves—a red linear motif in La Pasie-

ga, (Cantabria), a hand stencil in Malatravieso (Extremadura), and red-painted large stalactites in Ardales (Andalucía) (Hoffmann et al. 2018a; 2019). Since no “modern” humans were present in the Iberian Peninsula before 42 Ka, these artifacts must have been produced by Neanderthals.⁷ At the Roche-Cotard Cave, Indre-et-Loire, France, different motifs were engraved or traced with fingers on soft limestone surfaces deep within the cave (Marquet et al. 2023). The cave entrance was sealed around 57 Ka, as dated by OSL, providing a *terminus ante quem* for the creation of these finger flutings. Additionally, uranium-series dating of calcite layers overlaying some of the markings yielded an age of approximately 75 Ka, placing their creation firmly within the Mousterian—a dating supported by the stone tools discovered in the cave. A crisscross pattern deeply incised by Neanderthals into the bedrock of Gorham’s Cave, Gibraltar (Rodríguez-Vidal et al. 2014), discovered after removing Mousterian layers, is dated to more than 40 Ka, an age preceding the arrival of *Homo sapiens* in the region.

Taken as a whole, the available evidence indicates that markings and paintings produced by Neanderthals do not substantially differ in number, visual complexity, variety of used raw material, and technical skills from those found in some regions of Africa between 110 Ka and 40 Ka. The currently known record of such artifacts begins later in Africa than in Europe and Asia, but there are more indications of long-term continuity (albeit intermittent) of techniques and design features. Abstract designs (Figures 9 and 10) engraved on bone and ochre pieces, or drawn with ochre “pencils” on stone (Henshilwood et al. 2018) are found at Blombos Cave, Klasies River, Klein Kliphuis, Sibudu, and Pinnacle Point, South Africa, where they date to between ca. 110–70 Ka (d’Errico et al. 2012; Henshilwood et al. 2009; Mackay and Welz 2008; Watts 2010). A single more recent example comes from the Kenyan site of Panga Ya Saidi (d’Errico et al. 2020). These designs disappear from the ar-



Figure 9. Engravings on ochre and ostrich eggshells dated between 100 Ka and 58 Ka found at Middle Stone Age Southern African sites. a-b) Blombos Cave; c) Diepkloof shelter (modified after d’Errico and Henshilwood 2011).

archaeological record in the following period, reappearing in the same regions, but engraved on ostrich eggshells used as flasks for water and other material, c. 66–58 Ka (Henshilwood et al. 2014; Texier et al. 2013); and later on *Achatina* shells (Bicho et al. 2018) and bone (d’Errico et al. 2012). Abstract designs then disappear again from the archaeological record, and do not reappear at African sites until a few thousand years ago.

The periodic disappearance of abstract designs from the record highlights that the emergence of symbolic practices was not a linear or irreversible process. Rather, it underscores the vulnerability of such practices to demographic fluctuations, ecological pressures, and cultural transmission thresholds (Derex and Mesoudi 2020; Scerri and Will 2023). This pattern suggests that while the cognitive potential for material signs expressing motifs, possibly with symbolic meanings, remained present, its material actualization depended on social and demographic conditions that were not always sustained. The reappearance of abstract designs thousands of years later thus reflects renewed opportunities for the stabilization and diffusion of

semiotic traditions, consistent with our broader argument that such practices arose polycentrically and episodically before becoming consolidated.

It has frequently been argued (e.g., Henshilwood et al. 2009; 2018; Joordens et al. 2015; Rodríguez-Vidal et al. 2014) that abstract designs evidence the intention to create meaningful signs (Mellet et al. 2019a; 2019b), or exemplify, in certain cases, symbolic systems (Henshilwood et al. 2009). The sparse nature and appearance of this record, however, has attracted competing interpretations. Hodgson (2006) has proposed a *resonance hypothesis*, according to which engravings emerged from perceptual biases toward geometric primitives (e.g., intersecting lines) rather than from symbolic intent. On his account, hominins distilled naturally occurring visual features into “tangible purified formats” that resonated with pre-existing neural dispositions. Spinapoli (2024) argues, along similar lines, that these engravings reflect individual expression rather than shared meanings and in a similar vein Tylén et al. (2024) contend that the structural properties of the earliest engraving do not support the requirements of symbolic cognition.

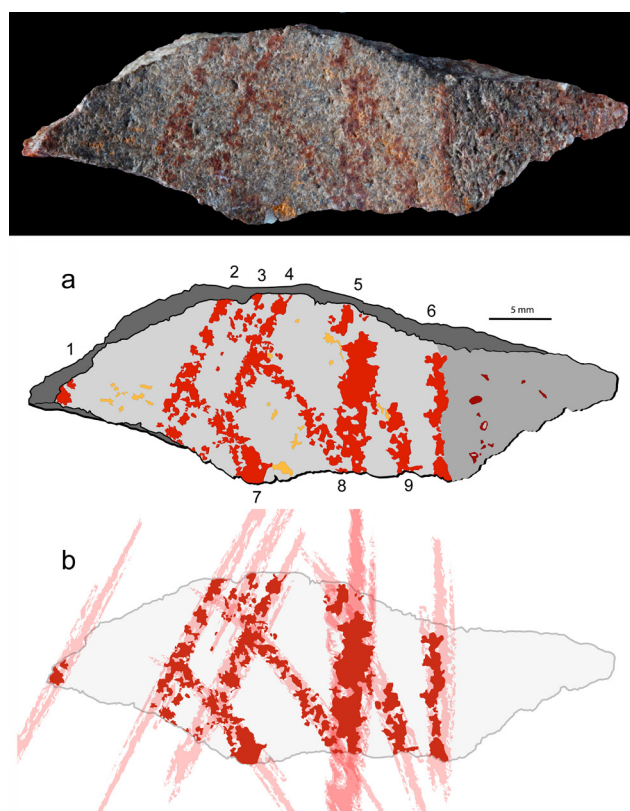


Figure 10. Top: photo of a fragment of silcrete found at Blombos Cave, South Africa, in a layer dated to c. 73 Ka, bearing a criss-cross pattern produced by an ochre crayon. Bottom: tracing of the red lines (a) and reconstruction of the pattern before breakage (b) (modified after Henshilwood et al. 2018; photo and drawings F. d'Errico).

Critics (e.g., Mellet et al. 2019) have pointed out, however, that individual neuropsychological explanations fail to explain why engravings recur across specific materials and sites, or why some engraved motifs are tiny and barely visible, more consistent with semiotic functions such as signaling group identity than proto-aesthetic enjoyment. Although the record of abstract engravings dated between 500 Ka and 50 Ka consists largely of isolated occurrences, some, such as the abstract engravings on ochre and on ostrich eggshells dated between 110 Ka and 58 Ka, both from southern African sites, and engraved cortices—the soft layer coating flint nodules—from Europe and the Near East, reveal persistent recurrence both in the choice and preparation of the medium on which the engravings were executed, and in the patterns engraved. This suggests that these practices, far from being random or incidental, were socially transmitted. These considerations undermine the resonance hypothesis proposed, which probably underestimates early humans' capability to imbue marks with meaning, especially when viewed within the broader context of proto-symbolic material culture associated with them, for example, their association with already complex body decoration.

Anderson (2012) offers a more nuanced account, synthesizing evidence for cross-hatched engravings on ochre, bone, and ostrich eggshell from Middle Stone Age contexts (100–60 Ka). She argues that such repeated geometric patterns engage the neural systems for vision, memory, and emotion, and that their significance lies not only in semiotic expression, but also in their neurological resonance as structured visual stimuli. From this perspective, their functional motivation is both psychological and cultural, suggesting that the early emergence of such designs may have scaffolded later symbolic meanings. Neuroimaging research by Mellet et al. (2019b) has demonstrated that the perception and processing of engraved abstract patterns elicit in modern humans higher-order brain regions associated with attention, visuospatial reasoning, and executive functions, rather than low-level visual processing areas. Mellet et al. (2019b) argue that these markings therefore required a level of intentionality and deliberate action inconsistent with Hodgson's (2006) claim that the artifacts emerged as a by-product of perceptual bias.

Although Mellet et al.'s (2019) results were obtained on contemporary participants, they are relevant for interpreting ancient engravings. While there may be differences in specific cognitive abilities, the fundamental neural architecture involved in visuospatial reasoning, attention, and executive function has deep evolutionary roots, shared to a significant extent with the hominins who produced these engravings, given their similar reliance on visual processing and fine motor control when, for example, heat-treating rocks to shape foliate points by pressure, blacken shell beads with complex procedures, produce delicate bone tools, or create distinct visual patterns by stringing shell beads in certain ways. The engravings required knowledge of the material's properties, appropriate tool selection, and skilled motor control. These actions suggest that hominins possessed cognitive capacities similar to those needed for complex toolmaking, which aligns with the neuroimaging findings of activated executive and visuomotor networks.⁸

Many of the earliest abstract designs indicate a high degree of technical skill and neuromotor control of precise, deliberate techniques, such as line juxtaposition and tool selection, implying learned, intentional behavior that goes beyond mere perceptual play. Analyses of these engravings show that their creators understood the properties of their material medium, carefully selecting materials and tools to achieve specific visual effects. Craftspeople used appropriate tools made of stone (or shark's teeth, as at Trinil), with consistent pressure and effort to create lines of uniform depth and spacing, suggesting an intentional approach rather than a casual, unconscious act. The alignment and juxtaposition of lines—seen in cross-hatched, parallel, and zigzag patterns—suggests that the engravers were deliberately creating structured designs. At Trinil, the engraved zigzag pattern was made visible by deeply incising with a point the dark brown organic layer covering the mineral part of the shell, called periostracum, to reach the underlying shell in order produce a white zigzag on a dark background. This marking procedure requires consider-

able effort. At Blombos several ochre pieces were carefully abraded by grinding to create flat, softer surfaces on which engravings could better visually stand out. At Gorham's Cave, Gibraltar, it has been shown experimentally that between 180 and 320 strokes were necessary to produce the deep grooves composing the criss cross pattern engraved on the hard dolomitic rock of the cave floor. At Ardales, Neanderthals used ochre collected at outcrops located outside the cave to paint in red a large dolomitic dome in spite of ochre of a different color and composition being available inside the cavity, indicating that the painting of the stalagmite was planned before entering the cave, possibly because the ochre of a brighter hue was preferred. Visiting the cave and coloring the stalagmite was performed repeatedly over time.

Experiments involving a substantial number of participants have shown that sequential notches produced by Neanderthals on the midshaft of a hyena femur at Marillac, France, were carefully spaced and the engraver made an effort to make the notches identical in shape, perfectly parallel and equidistant, reaching a level of visual consistency unmatched by modern experimenters who were asked to put every possible effort to mimic the arrangement present on the archaeological object (d'Errico et al. 2018). Systematically engraving abstract patterns covering the complete surface of the ostrich eggs, as recorded at several southern African sites, certainly required a high degree of focused attention and manual dexterity. The resulting patterns, made clearly visible on eggs perforated to be used for a prolonged period of time as containers were certainly visible to other members of the group, contradicting the idea of the engraving being used as spontaneous, momentary, and unplanned activity. In contrast, the same patterns or types of engravings appear in multiple archaeological contexts, sometimes spanning considerable distances and time periods. For instance, consistent cross-hatched engravings found on ostrich eggshells and ochre fragments in Southern Africa suggest an intentional continuity of design, implying that they served a semiotic function within these societies.

Malafouris (2021, 2023, 2025) situates abstract engravings within *Material Engagement Theory (MET)*, emphasizing that meaning emerges through embodied interaction with materials rather than through the externalization of internal representations. In this view, early engravings are primarily to be seen as the outcomes of enactive engagements with surfaces and tools, which shaped human becoming. MET enriches debates by highlighting the constitutive role of materiality in cognition, but can be criticized for under-specifying whether and when such marks should count as signs with communicative functions, rather than as traces of skilled material engagement alone.

We concur with Malafouris (2021) and others (Bender 2020; Cerulo et al. 2021; Lizardo et al. 2021) on the central importance of the materiality of the sign vehicle in shaping semiotic practice and human symbolic evolution. However, there is a danger that the account of enactive signification advanced in MET is seen as rejecting as intrinsically

theoretically flawed any interpretation of early engravings that attributes to them a sign status beyond the indexing their production and the process of human becoming itself. Such interpretations are assumed by MET to be necessarily rooted in a classical cognitivist approach to symbolization that views material signs as externalizations of internal representations. We have also rejected this theoretical framework, but unlike MET we have offered an account of the meanings of signs that recognizes their situatedness in the socio-cultural world, as well as the individual embodied activity, of the sign-producer. The MET approach can be criticized, then, for its focus on a general theory of embodied cognition in the production of material culture (the technosphere), without resolving the interpretative challenges posed by its intersection with (proto-)symbolic culture (the semiosphere). MET leaves unresolved, then, whether early engravings were signifying artifacts or non-significant outcomes of practical engagement. The strength of MET lies in providing a philosophically grounded framework for understanding human-material interactions; its weakness is a lack of the sematological analysis needed to distinguish between the creation of material signs and other forms of creative activity. MET undoubtedly enriches the discourse on early material culture, but it can be criticized for isolating embodied (co-)agency from the communicative practices that were simultaneously evolving into discursive conventions.

Tylén et al. (2024) adopt a related affordance-based perspective (Gibson 1979) on the earliest engravings, analyzing them as products of material engagement with interfaces that afford specific perceptual and interpretative responses. They propose that the engravings' material properties, patterns, and the surfaces on which they are inscribed guide human interaction and recognition.⁹ In their experiments, Tylén et al. explore how modern participants perceive and interpret these early engravings, aiming to establish whether they present the necessary affordances for being recognized as discrete symbols. In a recent study (Pagnotta et al. 2024), Tylén's team presents an ambitious protocol to investigate how symbolic meaning in early engravings may emerge. Their framework adapts methods from experimental semiotics to test whether participants perceive simple abstract patterns as carrying meaning. While this is a valuable methodological contribution, the protocol has several limitations. The authors have not yet provided experimental results to substantiate their view. This limits their contribution to a theoretical framework rather than an empirical advance. While protocols are valuable, their significance hinges on their execution and outcomes, especially in a field as interpretatively complex as prehistoric symbolism. The experimental stimuli that they present are far less complex than some of the more remarkable engravings found at Blombos Cave, such as cross-hatched designs or patterns on ochre. These simpler experimental drawings risk reducing the complexity of prehistoric artifacts to generic shapes, potentially skewing participant responses. The protocol does not address the fact that some Blombos engravings occur on fragmen-

tary pieces. In several cases these fragments are remnants of larger, more complex patterns, suggesting that prehistoric viewers might have interpreted the designs in ways difficult to replicate with isolated fragments. The problem is even more pressing in the case of the engraved ostrich eggshells. The patterns that have inspired their protocol try to mimic what is observed on small fragments of engraved eggshells. Originally, however, these eggshells were fully engraved, meaning that the designs would have been perceived as part of a coherent and continuous pattern wrapping around a three-dimensional surface. This volumetric context would have created an interplay of light, shadow, and spatial arrangement, allowing viewers to apprehend the designs as unified motifs, potentially with symbolic meaning or practical significance. Presenting simple motifs on a flat surface removes this spatial coherence, reducing the engravings to disconnected patterns that no longer align with their original context.

Comparison with analyzing a random swatch of the Mona Lisa illustrates this point—a fragment of the painting, divorced from its broader compositional unity, would fail to convey the intentionality, emotional resonance, or cultural significance of the complete work. Similarly, an ostrich egg with continuous engravings might have served as a visual, tactile, and symbolic artifact, whose significance could only be fully appreciated in its intact form. Pagnotta et al. (2024) also focus exclusively on visual perception, neglecting the embodied skill and knowledge required to produce the engravings. Experimental archaeology and neuroimaging studies, such as Salagnon et al. (2022), demonstrate that expertise in the production process enhances recognition and understanding of engravings. Their fMRI results show significant differences in brain activity between expert archaeologists and laypeople when interpreting marks, emphasizing the importance of production familiarity. Experts exhibited greater activation in the ventral occipitotemporal cortex and related integrative visual areas, reflecting their ability to recognize intentional patterns versus natural ones. Both experts and laypeople activated the salience network when uncertain about a mark's origin, but the experts' responses were more consistent due to their familiarity with intentional engraving processes. It is reasonable in this light to maintain that the Pagnotta et al. protocol oversimplifies the context, medium, and cognitive processes involved in prehistoric engraving interpretation.

An important limitation of all laboratory experimental studies (even of actual engraving specimens) with present-day, WEIRD¹⁰ (Henrich et al. 2010) participants is that they lack the cultural and contextual knowledge that lends meaning to these material signs. Members of contemporary Indigenous societies often understand simple engraved patterns in ways that differ significantly from WEIRD perceptions. A striking example is the *Kene Kuĩ* graphic art of the Huni Kuĩ communities of lowland Amazonia, employed in weaving, basketry, body painting, ceramics, hammock production, beadwork, and other practices, and officially designated as a Cultural Heritage of Brazil:

“Kene graphics possess a distinctive stylistic unity, marked by an aesthetic balance between symmetry and asymmetry, figure and background, using elaborate geometric patterns that narrate stories and reflect a rich and complex cosmology. Traditionally, the creation of kene is predominantly carried out by women, who hold the role of ‘aĩbu keneyá’ (masters of kene), transmitting knowledge through oral practices, songs, and rituals. Learning kene also involves observation and a connection with the ‘yuxibu’ (forest spirits), who inspire and guide the graphic creations” (Pastana 2025).

Where the naïve observer sees only elaborate geometric patterns, the Indigenously educated knowledge holder ‘sees’ snakes and other beings of the forest, whose appearance and acts are interpreted in the context of intergenerationally transmitted narratives.¹¹

Examples such as this abound in the ethnographic literature, and are found in all parts of the world. Gourds and pottery often embody meanings related to status, lineage, or spiritual beliefs, which may be imperceptible to outsiders without contextual understanding (Hodder 1982). North African Berber crafts incorporate geometric patterns such as lozenges, triangles, and dots, which function both as decorative and protective symbols, understood within a cosmological framework not apparent to a modern, non-indigenous observer. San hunter-gatherers make small incisions on arrow points that function as conventional material signs recognized and understood based on shared knowledge and experience (Wiessner 1983; see also Backwell and d’Errico 2021). In Papua New Guinea, small symbolic marks on tools and objects often signify ownership, clan identity, or ceremonial status. These inscriptions are comprehensible only to individuals immersed in the cultural context, underscoring the importance of social learning and shared traditions in interpreting such signs (Munn 1992).

In conclusion, it is our contention that the deliberate production of engravings must from the start have been implicated in the emergence and evolution of *both* technospheres *and* semiospheres. The abstract engravings, drawings, finger flutings, and paintings found at African Middle Stone Age and Eurasian sites older than 45 Ka share notable traits. Though limited in number, and appearing sporadically across time and space, they reveal technical and neuromotor precision that strongly indicates the intentional creation of visuo-spatial motifs, not random doodlings. Their regional specificity and ephemeral nature suggest that they were embedded in local symbolic practices and that their persistence depended on local ecological conditions, demographic thresholds, and transmission structures. This variability indicates that symbolic practices were socially learned and shared, but fragile; they could flourish where networks supported their transmission, and fade where conditions were unfavorable. The geographic and chronological distribution of these practices shows patterns of both consistency and isolation. Specific engraved motifs appear repeatedly at sites in Southern Africa,

including engraved ochres and engraved ostrich eggshells, and the Near East and Europe with engraved bone and cortexes. However, many other examples of early engravings are unique to single sites and do not suggest long-standing symbolic traditions. This variability hints that these marks may have been of spatio-temporally local significance, or served as emblematic signs of ownership or affiliation within small social groups, rather than instantiating enduring cultural conventions. The engraved ostrich eggshells from southern Africa are the only objects on which the engravings occur on functional artifacts. In all other instances (engraved ochre, bone, stone, finger flutings on cave walls, engravings on cave floor, paintings on stalagmites) they cannot be interpreted as decorations on tools.

The significance of early semiotic artifacts lies in their ability to convey meaning beyond the immediate practical context, suggesting that by producing and recognizing them, hominins were expanding their biocultural niches to include material markers of personhood, identity, and belonging (cf. Malafouris 2024). Their variability and discontinuity across time and space suggest that these visual expressions did not radiate out from a single cultural center but rather developed independently in multiple regions. This polycentric origin implies that early humans in different groups or locations may have invented these expressions in parallel, driven by local environmental and social needs. Rather than a simple linear evolution, the evidence points to a mosaic of innovation and experimentation. A plausible view is that early abstract engravings should be considered as motifs that were precursors, perhaps even instances, of emblematic signs, rather than fully developed symbols. In later human societies, we observe how symbolic practices diversified to marking objects as participants in complex symbolic systems including abstract and transcendental entities and relationships. The lesson we can draw from the role of abstract visual art in contemporary societies is that, while visual motifs may in some cases be ‘meaningless’ patterns, they can also be both emblems of cultural identity and constitutive parts of shared universes of discourse, ranging from markers of affiliative identity to complex symbolic structures combining traditional ecological knowledge (Pierotti and Wildcat 2000), cosmologies, social relations, and cultural ontologies.

4.6. FIGURATIVE REPRESENTATION

Since their discovery in 1994, originally dated to 32–20 Ka (Quiles et al. 2016), and later updated to between 36.5 Ka and 33 Ka, the paintings of the Chauvet Cave, France, along with the ivory figurines from the Swabian Jura, 40–33 Ka (Conard 2003), were long considered to be the earliest instances of figurative representations. The earliest figurative representations from Africa, consisting of animal figures executed in ochre and charcoal on stone slabs found at the Apollo 11 rock shelter, Namibia (Rifkin et al. 2015; Wendt 1975), dated to c. 30–28 Ka, are more recent than the Chauvet Cave paintings. However, in 2014, Uranium-series (U-series) dating of rock painting in Maros-Pangkep, Sulawesi (Indonesia), revealed an antiquity of at least 39.9 Ka

for a hand stencil and 35.4 Ka for a painted depiction of an animal (Aubert et al. 2014). More recent U-series dating has yielded minimum ages of 40 Ka for figurative animal paintings in Kalimantan and 45.5 Ka in Maros-Pangkep. Very recently (Brumm et al. 2021; Oktaviana et al. 2024), using the same method, a minimum age of 51.2 Ka has been attributed to a newly described scene at Leang Karampuang in South Sulawesi, Indonesia, depicting human-like figures interacting with a pig. This is significant because, unlike the Chauvet paintings, it shows what appears to be a scene involving the animal and humans, rather than associated “portraits” of animals alone, suggesting that the scene is a constituent of a narrative.

This scene pushes back the timeline for the emergence of figurative representations, suggesting that early humans in Southeast Asia may have engaged in this type of symbolic practice before their European counterparts. The chronological and geographical divide between the earliest instances of figurative depictions in Africa, Europe, and Asia, and the absence until recently of such expressions in many regions of the world, is consistent with our thesis that geographic isolation and social needs have stimulated polycentric invention, convergent evolution, and eventual cultural hybridization. To take a much later example, different writing systems and numerical systems emerged *independently* around the Mediterranean, in Mesoamerica, and in China (see HOLO 2: Arbib et al. 2027 [this issue]). It is only in the last two centuries that scholars have been able to assess them as variations on a single dramatic extension of human biocultural niches.

Figurative representations are widely regarded as the most reliable archaeological proxies for symbolic thinking and language (Coolidge and Wynn 2005; Deacon 1997; Donald 1993; Dubreuil and Henshilwood 2013; Sterelny 2011). As repeatedly observed in traditional societies (Zubieta 2016, 2022), creating and sharing figurative depictions involves instruction, collaboration, and demonstration, implying a need for precise, structured communication. This need for shared knowledge and understanding requires a language advanced enough to support complex symbolic cultural transmission, with vocabulary and structures for teaching techniques, describing forms, and conveying stories or meanings attached to the figures. Their production and perception requires the ability to conceive and reproduce images that stand for something beyond their literal form, such as animals or human figures. Many figurative depictions hold narrative elements, such as animals in specific poses or recurring motifs, which could indicate stories, myths, or cultural beliefs (for an extended discussion, see Davidson 2025).

Caution is necessary, however, in extrapolating from visual representations to the complexity of the languages spoken by their makers. The “grammar” of putting marks and patches of color together to create a scene is very different from that for combining actions to perform a practical task, and even more so from the grammars of EMLs that have not only a lexicon but also complex compositional semantics. Creating a figurative depiction demands, how-

ever, the ability to mentally abstract from the immediate environment, as well as to project an idea or image into a physical form. Sequential visual narratives depicting spatio-temporally extended events depend on such cognitive displacement. Zhang et al. (2024) argue that displacement as a linguistic design feature evolved from more general cognitive abilities for representing non-immediate scenarios. Recent research on multimodality emphasizes that visual communication constitutes an expressive system in its own right, with organizational principles distinct from the grammar of spoken languages (Schilperoord 2024). It is possible that early humans could, in principle, craft and comprehend visual narratives without necessarily commanding the full set of grammatical devices characteristic of EMLs. The archaeological record thus reliably documents the emergence of displaced cognition, but not necessarily of fully grammaticalized EMLs.

Merker (2002, 2015) has stressed that both language and music form a *Humboldt system*, a generative system based on the so called “particulate principle” in which unlimited pattern diversity is generated through combinations among a finite (typically small) set of non-blending elements. Music differs from languages in that its smallest units do not carry conventional referential meanings (Jackendoff 2009). Its power lies rather in its combinatorial structuring of sounds, which can scaffold memory, coordinate collective activity, and reinforce social cohesion without referential semantics. Here, we draw attention to the paradox that drawings and paintings are both more powerful than language—in that they allow the unlimited reshaping and assemblage of diverse meaningful elements to convey new meanings—and more limited, in that by employing a relatively limited (though potentially very large) range of non-blending elements a language offers less direction to the receiver as to its intended meaning.¹²

We argue that visual narratives do, nonetheless, mark a significant step in human symbolic evolution. The stylistic and thematic consistencies of much figurative art imply a shared understanding within groups or across regions, underpinned by a shared means of communication sufficiently complex to convey cultural norms and aesthetics, and to negotiate meaning and interpretation within a group context. An ability to produce and understand narratives that dissociate depicted event sequences and their order of mention, attribute causality and motivation, mark protagonism and antagonism, and express embedded temporal relationships, would be necessary to explain or interpret such depictions. These are all hallmarks of EMLs. Through this ability to represent, combine, and innovate, early humans opened the door to new representational spaces, consolidating the uniquely human capacity for linguistically mediated symbolic culture—the foundation of the social imaginary.

4.7. SUMMARY: INTERPRETING MATERIAL SIGNS

The archaeological evidence reviewed above points to a fragmented cultural landscape where semiotic innovations

first arose independently and polycentrically, influenced by specific ecological and social conditions. This fragmentation contrasts with later periods, where cumulative culture and broader networks facilitated the persistence and dissemination of symbolic behaviors. The recurrent emergence and disappearance of semiotic practices in the archaeological record probably arose from fluctuating demographic or ecological conditions. Recent models suggest that population size and structure play crucial roles in whether cumulative cultural evolution can be sustained—smaller or fragmented populations may innovate but fail to maintain and transmit complex practices over time (Drex and Mesoudi 2020; Scerri and Will 2023). As Stibbard-Hawkes (2025) argues, contemporary hunter-gatherer material practices show that cultural complexity can be highly variable, without implying differences in underlying cognition. Our interpretation of symbolic practices therefore situates their appearance and disappearance within a dynamic framework of population structure, demography, and cultural transmission, rather than treating them as straightforward reflections of cognitive thresholds.

The ephemeral nature of early proto-symbolic practices aligns with broader patterns of human evolution, emphasizing gradual shifts towards increased cultural exchange and integration over time. Our account of the emergence of symbolic practices suggests that, as hominins complexified their cultures, the expanding technosphere was augmented by conventionalized meanings that became increasingly specific to a group (or interacting groups), rather than being directly tied to the genetic basis of a species. Meanings that were inherent in the dynamics of interaction with the spatio-temporally local environment became increasingly extended by symbolic values that went beyond the spatio-temporally immediate survival value of social learning. Hovers and Belfer-Cohen (2024: 495) have recently emphasized the variability and contextual complexity of symbolic practices in the Levantine Middle Paleolithic, arguing that there, as elsewhere, “[T]he coevolution of social processes and symbolic culture involved complex feedback loops whereby the expansion of social units and networks entailed increasing reliance on symbols.” This perspective resonates with the arguments advanced here, consistently with our emphasis on the mosaic and context-dependent nature of semiotic innovation, and the role of niche expansion and hybridization in shaping diverse pathways to symbol use.

5. LOOKING AHEAD

We have proposed a co-evolutionary approach to human origins, linking changes in the human organism to biocultural niche expansion. The data we have reviewed contradict any notion of a unique origin of cultural complexity, modern cognition, or Evolutionary Modern Languages (diverse as they may be) in either Southern or Eastern Africa. There is no clear correspondence between the emergence of our species, the invention of specific praxic technologies, and the appearance of specific types of material sign, all of which are often considered to be hallmarks of “modern”

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cognition. Archaeological, biological, and cultural evidence supports a complex, multi-regional emergence of modern human cognition and symbolization, pointing to a gradual, polycentric and asynchronous evolution of symbolic practices and languages across different human populations, made possible by the pre-existence of a *language-ready brain* (Arbib 2012). The core of our approach to human origins and language origins is that language did not evolve as a “faculty” separate from other human abilities; rather the biocultural evolution of symbol-readiness, language-readiness and construction-readiness were intertwined, as were the polycentric paths of cultural evolution that extended the range and complexity of the semiospheres and technospheres of diverse human biocultural niches.

Unlike other approaches to human evolutionary niche construction and its relation to language origins (Odling-Smee and Laland 2009; Stutz 2014), we theorize *language itself* as a constituent biocultural artifact/niche within a semiotically mediated human biocultural complex, that “includes the information, *both* in the genome *and* in the niche, that is required to learn how to exploit it” (Sinha 2024: 220).¹³ As such, language is *integral to*, rather than a consequence, or epiphenomenon, of the biocultural evolution of *enlanguaged* human cognition and action (Dreon 2025). This approach contrasts with accounts that see language as an autonomous faculty, having an evolutionary history independent of other aspects of human evolution. This is not to deny that the emergence of language introduced profound changes in hominin behavior and cognition, but it did so neither suddenly, nor out of nowhere, behaviorally, socially, or neurocognitively. Languages evolved as one, perhaps the fundamental, mediational semiotic vehicle for the creation and transmission of the complex, integrative meaning systems that we designate the *social imaginary*, whose emergence and elaboration were synergistically intertwined with the evolutionary pathways to Evolutionary Modern Languages.

In HOLO 2 (Arbib et al. 2027 [this issue]), we shall aim to identify the key evolutionary steps that enabled hominins, starting from our last common ancestor with the great apes (LCA-ga), to develop the capabilities necessary for symbolic communication and language, laying the groundwork for the cultural evolution of humans who constructed complex material and symbolic cultures and modes of communication. We propose that a capacity for complex imitation and action recognition supported symbolic modes of pantomimic, proto-, and early linguistic communication, with protolanguages of restricted compositionality already in place well before 400 Ka. Evolutionarily Modern Languages resulted from subsequent gradual and successive processes of grammaticalization (Heine 2023; Heine and Kuteva 2007; Kuteva and Heine 2024; see also Table 1, HOLO 2, and §4.1 HOLO 2) and lexicalization of multiplying semantic domains. This led, perhaps as far back as 160 Ka and at the latest 50 Ka, to languages with a systemic complexity equivalent to those that we know today.

¹This article is HOLO 1 (Part 1) of two complementary articles by the same authors (the other is referred to as HOLO 2) addressing the evolution of human material and symbolic culture, and especially language. We intend each article to be a stand-alone piece suitable for a multidisciplinary readership, but acknowledge that each will explore themes that are more fully explored in its companion article. Here and elsewhere, we mean by “language” any system equivalent in complexity to *Evolutionarily Modern Languages*, the kind of languages people speak today, all of which, despite typological variations in the complexity of subsystems, are of essentially equivalent complexity (Bentz et al. 2023).

²Plunkett and Sinha (1992) argue for an epigenetic developmental interpretation of connectionist computational modelling in artificial neural networks (see also Elman et al. 1996; Plunkett et al. 1992).

³The relationship between cumulative cultural-technological diversity and cumulative complexity is not clear (Buskell 2022). The cultural variability observed in artifact use by chimpanzee societies (Boesch et al. 2020; Kalan et al. 2020; Tutin et al. 2001; Whiten et al. 1999), and at chimpanzee archaeological sites (Haslam et al. 2017; Mercader et al. 2007), suggests that cumulative diversity through cultural transmission may date to the last common ancestor of extant great apes. Capuchin (*Cebus*) monkeys, by contrast, acquire skills in palm-nut cracking through observation, but only after years of practice, with no observable diversification between groups, although some *Cebus* groups have this tradition, while others do not, and there is evidence that stone anvils are used across many generations (Arbib et al. 2023; Frigaszy et al. 2013). Cumulative cultural diversity is not confined to primates, being found, for example, in tool making by New Caledonian crows (Hunt 1996; Taylor and Jelbert 2020).

⁴The traditional distinction between material and symbolic culture is open to criticism, but it remains useful to distinguish between artifacts implicated in constructive praxis (the constituents of the technosphere), and those implicated in communication through signs (the semiosphere); the latter including both material artifacts, such as ornaments, and communicative systems, including language.

⁵Its functional use, mixed with organic adhesives, to haft stone tools, especially those used for cutting, may have considerably predated this (Ryzhov et al. 2022).

⁶Describing all these findings in detail is outside the scope of our paper.

⁷These results have been questioned by casting doubt on the reliability of the dating method or by proposing that, in the case of the Ardales cave, the red marks on the speleothems could have a natural origin (Aubert et al. 2018; Pearce and Bonneau 2018; Pons-Branchu et al. 2020; Slimak et al. 2018; White et al. 2019). The authors of the original study have responded to these criticisms by reaffirming the validity of their dating results (Hoffmann et al. 2018b; c; 2019; 2020) and the newly published analysis of the red material on the Ardales speleothems clearly shows the red residues coloring the calcitic dome are an anthropogenic pigment, probably brought into the cave after being collected by Neanderthals at an outside ochre outcrop (Pitarch-Martí et al. 2021).

⁸An additional criticism, shared by Froese et al. (2014), that Mellet et al. (2019a) raise against Hodgson’s hypothesis is its lack of empirical verifiability and its reliance on theoretical assumptions that cannot be directly tested or demonstrated in prehistoric contexts. Mellet et al. argue that studying modern human brain activity in response to ancient engravings or analogous stimuli can generate testable hypotheses about the cognitive and neural processes involved in producing such engravings.

⁹The notion of *constructed affordance* is important in the articulation of niche construction theory in the context of human material, linguistic, and symbolic artifactual production, but we do not have space here to explore this further (see Sinha 2009, 2024, 2025).

¹⁰Western, Educated, Industrialized, Rich and Democratic.

¹¹Personal communication, Joaquim Kaxinawa and Vera da Silva Sinha, September 2025.

¹²Although the importance of music lies outside our present scope both of this paper and of HOLO 2 (Arbib et al. 2027 [this issue]), we note here the discussion of music, language and the brain (Arbib 2013)

that includes treatments of music as integrated/co-evolving with action in dance and ritual and their co-evolution in the soundscapes of the biocultural niches (Cross et al. 2013; Lewis 2013), not just as a separate system of sounds. We may note the capacity of language to express and support reasoning with propositions, and the capacity of music to stir emotions (a capacity that language shares, but in a different fashion) and create soundscapes.

¹³The *genome* should be understood in this context as encompassing various hominin populations (Zilhão et al. 2024), traditionally interpreted as separate species (Meneganzin and Stringer 2024). Recent genetic evidence suggests that these populations are better understood as subpopulations within a largely interconnected genetic pool, reflecting a dynamic web of gene flow and admixture that shaped the evolutionary trajectory of human biocultural complexity.

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AUTHORS' CONTRIBUTIONS

Francesco d'Errico and Chris Sinha are mainly responsible for the text, with contributions from all other authors to parts of the text and to the ideas and evidence therein.

DATA AVAILABILITY AND PERMITS

All the data presented are available in the paper text and figures.



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