Journal of Human Evolution 179 (2023) 103358

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

The revolution that still isn't: The origins of behavioral complexity in *Homo sapiens*

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A R T I C L E I N F O

Article history:
Received 27 July 2022
Accepted 14 March 2023
Available online xxx

Keywords:
Middle Stone Age
Early Stone Age
Cultural evolution
Stone tools
Modern humans

A B S T R A C T

The behavioral origins of *Homo sapiens* can be traced back to the first material culture produced by our species in Africa, the Middle Stone Age (MSA). Beyond this broad consensus, the origins, patterns, and causes of behavioral complexity in modern humans remain debated. Here, we consider whether recent findings continue to support popular scenarios of: (1) a modern human ‘package,’ (2) a gradual and ‘pan-African’ emergence of behavioral complexity, and (3) a direct connection to changes in the human brain. Our geographically structured review shows that decades of scientific research have continuously failed to find a discrete threshold for a complete ‘modernity package’ and that the concept is theoretically obsolete. Instead of a continent-wide, gradual accumulation of complex material culture, the record exhibits a predominantly asynchronous presence and duration of many innovations across different regions of Africa. The emerging pattern of behavioral complexity from the MSA conforms to an intricate mosaic characterized by spatially discrete, temporally variable, and historically contingent trajectories. This archaeological record bears no direct relation to a simplistic shift in the human brain but rather reflects similar cognitive capacities that are variably manifested. The interaction of multiple causal factors constitutes the most parsimonious explanation driving the variable expression of complex behaviors, with demographic processes such as population structure, size, and connectivity playing a key role. While much emphasis has been given to innovation and variability in the MSA record, long periods of stasis and a lack of cumulative developments argue further against a strictly gradualistic nature in the record. Instead, we are confronted with humanity's deep, variegated roots in Africa, and a dynamic metapopulation that took many millennia to reach the critical mass capable of producing the ratchet effect commonly used to define contemporary human culture. Finally, we note a weakening link between ‘modern’ human biology and behavior from around 300 ka ago.

1. Introduction

The cultural dimension of human evolution has preoccupied archaeologists and anthropologists since the inception of these disciplines and remains a topic of intense debate today. The increasing behavioral complexity of large-brained hominins from the Middle Pleistocene onward is typically measured in terms of contemporary human behavior (i.e., the ethnographic present), such as the use of abstraction, symbolism and language, hyper-sociality and altruism, the creation of art, and cumulative culture (Wadley, 2001; Dunbar, 2003; Henshilwood and Marean, 2003; Shultz et al., 2012; Conard, 2015; Marean, 2016; Wynn et al., 2016). At the turn of the 21st century, the debate on where, when, and how the roots of these behaviors appeared was radically shaped by a new model that placed the major milestones in the development of our species within a Middle to Late Pleistocene gradualist context in Africa. Far from being an Upper Paleolithic ‘revolution’ in the European Ice Age that had dominated scholarship at the end of the 20th century (e.g., Mellars, 1989, 1994; Mellars and Stringer, 1989; Straus, 1996), McBrearty and Brooks (2000) showed that the emergence of symbolic material culture, regional technological diversification, the use of diverse raw materials, expanded social networks, and economic intensification could all be traced back

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https://doi.org/10.1016/j.jhevol.2023.103358

among our species in Africa, at a much earlier time frame. Specifically, these behaviors were all linked to the Middle Stone Age (MSA), now known to be the first and longest-lasting stone tool (lithic) material culture to be associated with our species (e.g., Hublin et al., 2017; Richter et al., 2017). At a time when human behavioral 'modernity' was inexorably linked to the Middle to Upper Paleolithic transition in Europe, McBrearty and Brooks (2000) blazed the way for a new and intensive focus on Africa and the MSA. This provided an urgently needed archaeological piece of the human origins puzzle just as paleoanthropological and genetic research increasingly pointed to a deep-time origin of *Homo sapiens* in Africa (e.g., Bräuer, 1984, 1989; Cann et al., 1987; Stringer and Andrews, 1988).

This body of seminal paleoanthropological, paleogenetic, and archaeological work has had a profound effect by framing the MSA as the cultural backdrop to the rise of *H. sapiens*, bringing into sharp focus the need to study MSA sites to elucidate the behavioral origins of our species. The shift is perhaps most evident in the fact that generally speaking, prior to the 1990s, 'high-profile' publications on the MSA were scarce, with scholarly attention on the African Paleolithic largely given to the Early Stone Age (ESA) and Later Stone Age (LSA). As an example, and considering this as a contribution to the special issue celebrating the 50th anniversary of the Journal of Human Evolution, we conducted a simple search for its online database from 1972 to 2020 for publications either with a focus on the MSA or those mentioning the term in the abstract or keywords. No relevant paper appeared between 1972 and 1980 or 1981 and 1990. Between 1991 and 2000, there were 24 papers on the topic (5% of $n = 529$ total research articles), the earliest focusing on the MSA at Die Kelders by Grine et al. (1991). In this age bracket, 2000 was a key year with 13 of 24 papers published, including the special issue on Die Kelders in South Africa (volume 38, Issue 1), and the McBrearty and Brooks (2000) article. Conversely, from the 2000s, this higher interest continues and increased markedly with 62 papers covering the MSA as a topic in JHE between 2001 and 2010 (8% of the $n = 769$ total research articles), and 83 between 2011 and 2020 (8% of $n = 1100$ total research articles). In addition to other landmark publications in high-ranking journals (e.g., Henshilwood et al., 2002), these data show that the MSA underwent a change from obscure to prominent regarding Paleolithic archaeology and research on human evolution more broadly.

Twenty-three years after the publication of the seminal McBrearty and Brooks (2000) paper in this journal, the origins of *H. sapiens* behavioral complexity remain a central topic of global research. But what has changed, and what more do we know? A generation's worth of archaeological investigation has unearthed a significant corpus of new data from which to consider the question of the origins of modern human behavior, and what the referents of this term are now considered to be. New empirical studies have also been accompanied by changing theoretical perspectives on how to best understand the significant changes happening during the MSA. In this contribution, we first provide an overview on some recent theoretical and conceptual developments on how to best view and trace the evolution of behavioral complexity in the archaeological record of early modern humans. Based on this discussion, we review relevant empirical findings since 2000 from the African record in different spatial regions. In a third step, by combining new conceptual ideas with the spatiotemporal patterns of evidence, we provide an updated panorama on the origins of behavioral complexity in the early phases of our species. Lastly, we discuss potential causal mechanisms of the observed patterns, promoting an interdisciplinary approach that takes into account multiple causal factors with a focus on demography to understand key changes and patterns in space and time. Instead of sticking to taxonomic boxes relating to archaeological periods, we focus on the general time frame ~500–30 ka in Africa, which encompasses the transition between the ESA and MSA, the emergence of the *H. sapiens* phenotype and most of the MSA record.

2. Conceptual changes: Modern packages, evolutionary scenarios, and trait lists

Paleoanthropological research around the theme of the origins of modern behavior can be broken down into discussions of (1) how, where, when, why, and if an 'assembling of the package of modern human behaviors in Africa' took place (as summarized by McBrearty and Brooks, 2000); (2) theoretical discussions on how best to conceptualize and interpret archaeological data informing on the evolution of behavioral complexity in *H. sapiens*; and (iii) epistemological treatments and discussions of trait lists.

Historically, the concept of 'cultural modernity' viewed within a binary framework of presence and absence has long dominated discussions on the behavioral evolution of our species. The concept derived from work on the beginning of the Upper Paleolithic and the distinction of 'modern' humans from Neanderthals, as assessed by a trait list based on a range of European archaeological materials (e.g., Mellars, 1989; Bar-Yosef, 2002). Initially, most discussions centered around the modern 'package' occurring at a single point in time, often envisioned as a big leap or 'revolution' in our evolution (Mellars, 1989, 1994; Mellars and Stringer, 1989; Straus, 1996). Klein (1994, 2000, 2008, 2009) subsequently formulated a similar view for Africa, proposing a sudden origin of behavioral modernity as a package at a late point around ~50–40 ka, and coincident with the origin of the LSA (see also Ambrose, 1998).

In a direct reaction to these revolution models, McBrearty and Brooks (2000) proposed a very different scenario of a long, gradual, and mostly cumulative process of incremental assembly of the modern package for *H. sapiens* within Africa, unfolding from their biological origins. Since 2000, the notion of the origin of our species cognitive and behavioral complexity arising at a single point in time as single 'package' of traits—at times summarized under the term of 'cultural modernity'—with its Eurocentric view has increasingly been criticized based on theoretical, methodical, and empirical grounds (Wadley, 2001; Henshilwood and Marean, 2003; Nowell, 2010; Shea, 2011; d'Errico and Stringer, 2011; Conard, 2015; Haidle et al., 2015, 2016; Wynn et al., 2016). For example, Conard (2005, 2008, 2015) favors a decentralized, heterogenic, and multiorigin pattern taking place over the late Middle and Late Pleistocene without a single epicenter in Africa. Further scenarios include a special focus on the rich southern African record during the Late Pleistocene (Parkington, 2001; Jacobs et al., 2008; Marean, 2011) and considerations of complex patterns in space and time that also encompass species other than *H. sapiens* in Eurasia (d'Errico, 2003; Zilhão, 2007; d'Errico and Stringer, 2011). At the same time, recent models have started to focus more on variability (Shea, 2011), flexibility (Kandel et al., 2016), or plasticity (Malafouris, 2010; Roberts and Stewart, 2018), rather than a 'master' switch event at some key threshold in time.

While gradualistic, polycentric interpretations of the record continue to be drawn even as new regions of Africa become better understood for their Pleistocene past, the fundamental tool of inference remains based on the appearance of particular traits at different points of time deemed to be in some way important for 'modernity.' This approach plays to the strengths of archaeology. Artifacts are interpreted as expressions of traits and capacities that are themselves interdependent manifestations of the cumulative effects of human cognitive evolution. However, to use the words of d'Errico (2003), what are the criteria for selecting the criteria?

Table 1 summarizes key traits referred to in important studies since 2000 to potentially track human cultural and behavioral evolution (e.g., McBrearty and Brooks, 2000; Henshilwood and Marean, 2003; Conard, 2015; Shea, 2011). These can be ostensibly grouped into traits that reflect (1) group identity and social networks; (2) personal and intragroup communication, codification, and shared beliefs; (3) social cohesion and inter-reliance; (4) planning, innovation, and experimentation; (5) ecological and dietary flexibility and the ability to be specialist 'generalists'; and (6) control and remodeling of landscapes and ecosystems.

The interpretation of these traits is typically linked to a body of middle range or bridging theory (see Botha, 2010; Haidle, 2014; Coolidge et al., 2016) and research in this direction has provided key conceptual advances since 2000. This body of work mostly derives from actualistic studies (sensu Binford, 1981) and involves ethnographic research on extant or recent hunter-gatherer societies but also experimental archaeology to establish archaeological correlates for behavioral and cultural complexity observed in the present. On top, several studies have sought to link the production of different kinds of products recognizable in the archaeological record—standardized forms, use of new raw materials and their transformation such in heat treatment or long production sequences of composite weaponry including hafting adhesives—to potential underlying cognitive abilities and processes as studied and inferred in recent humans (e.g., Wadley et al., 2009; Lombard and Haidle, 2012; Wadley, 2013; Haidle, 2014; Stolarczyk and Schmidt, 2018; Coolidge et al., 2016).

Group identity and social networks are a hallmark of extant human societies and are ethnographically documented around the world, from computer-based social networks to those of modern hunter-gatherers (e.g., Wiessner, 1983). At their core, dispersed social networks foster co-reliance and the pooling of risk—observations that have greatly impacted archaeology interpretations of Pleistocene artifacts (Gamble, 1982; McCall, 2007; Tostevin, 2012). Such work also showed the pitfalls of making assumptions based on technological similarities across assemblages. For example, Wiessner (1983) also showed that mutually unintelligible non-risk-sharing San groups of the Kalahari shared 90% of their material culture as a result of shared environments. For these reasons, archaeological focus on recognizing social networks has tended to search for evidence of long-distance transfers, and the standardization of point forms in particular (Table 1). Evidence for some long-distance transfers of raw material exists from slightly before 300 ka (Brooks et al., 2018). The inland transfer of marine shells, whether intentionally perforated or not, also points to other forms of material transfer by the Late Pleistocene (d'Errico et al., 2009). Although this is not direct evidence of social networks, the idea that they existed is also reflected in the standardization of regionally distinctive MSA point forms (e.g., Scerri, 2013a; Wadley, 2015). The theory behind this view lies in ethnographic work (e.g., Wiessner, 1997) showing that points are, by their nature, taken onto the landscape for hunting reasons. It is in this wider landscape that encounters with other hunting groups are most likely, and therefore where the need for emblematic social signaling arises (Lechtman, 1977; Binford, 1989; Sackett, 1990; Tostevin, 2012). The combination of the long-distance transfer of different materials, including exotic ones, and the standardization of point forms, therefore, presents good evidence for the existence of social networks and risk-pooling groups. Standardization in other tool forms, such as (microlithic) backed pieces and their spatial dispersion, has likewise been argued to reflect underlying mental templates related to social connectivity and increased long-distance social ties (Wurz, 1999; Way et al., 2022).

Personal and intragroup communication, the codification of referents, and shared beliefs represent an entirely different dimension of complex culture and require abstract thinking. If networks and emblematic signaling focus on intergroup cooperation or recognizing the lack of it, other lines of evidence point to within-group communication and shared beliefs. For example, intentional burial with 'goods' such as wrappings (e.g., Martinón-Torres et al., 2021) may indicate this, although further evidence is required to make arguments for systematic practices beyond emotional attachment to the dead. Other lines of data, such as collections of sets of objects like marine shells (Gamble, 2007;

Table 1
List of key traits thought to reflect the hallmarks and spectrum of behavioral complexity or 'modern behavior' and respective bridging theories (see text and e.g., McBrearty and Brooks, 2000; Henshilwood and Marean, 2003; Conard, 2015).

Trait	Inference	Bridging theories
cLong-distance transport, e.g., of raw material, shells, etc.	Social networks, exchange	Social groups pooling risk in situations of demographic stress
Standardization of regionally distinctive artifacts and tool forms (e.g., point forms, backed pieces)	Social networks, signaling of emblematic style	Representation of group identity, shared concepts and signaling potentially linked to risk-pooling groups
Notching, incision, patterns, art	Intentional designs, abstract thinking, intragroup codification, and symbols with language?	Representation of identity (personal or group), the intersection of habitual disposition and concrete social conditions that create meaningful visual codes
Collections of shells, some intentionally perforated	Personal ornamentation, esthetics, symbolism? collections of sets	Personal ornamentation points to sense of identity of self vs. others, collections indicate concepts of esthetics and value
Intentional burial	Coping mechanisms for grief, shared values, belief systems	Mortuary treatment relates to bonds of affection and group identity. Burial ethnographically also relates to systems of shared belief
Artifact diversity in form, material and method; hafting and composite tools; pigment use	Task specialization, innovation, teaching, planning depth, memory, abstract thought?	Task specialization drives social cohesion, and may also require language. Diversity in use of forms, materials and methods including composite products implies advanced cognitive processes, increased creativity and problem-solution distances, and expanded subsistence and lifeways
Structured living spaces	Group cohesion, planning depth, social order	Denotes an understanding of the optimal organization of space relative to lifeways and subsistence
Diet breadth	Adaptability, flexibility, and plasticity of behavior	Humans are 'generalist specialists' whose specialty is to rapidly adapt to new environments and foods
Expanded ecological niche	Innovation, planning, experimentation, flexibility, and plasticity of behavior	Ability to test and learn new adaptive strategies and pass these horizontally and vertically within group
Diverse use and control of fire	Cooking, heating including heat treatment of raw materials, control of plant life and ecosystems	Using fire to control landscapes, food, and raw material demonstrates unprecedented control of the natural environment
Seasonal habitation or resource exploitation	Planning depth, understanding of cyclicity and periodicity	Ability to project and plan into the future based on modeling of the past

d'Errico et al., 2009; Wilkins et al., 2021) whose rarity may even communicate their worth as 'something special,' may also point toward shared concepts of esthetics and value. Finally, artifact diversity in used materials, form and manufacture point toward increased creativity and the sorts of required specialisms that promote social cohesion within groups (e.g., collection and flaking of raw material, manufacture of bindings and resins, production of wooden shaft, etc.). This includes the capacity to combine materials not found together in nature in new ways in long procedural chains of action and transform them such as in compound adhesives or bow-and-arrow sets, involving multitasking and increased working memory (e.g., Wadley et al., 2009; Lombard and Haidle, 2012; Coolidge et al., 2016). Taken together, these mixtures of traits provide good evidence for the accumulation of cognitive capital, often expressed as intragroup strategies. Other classes of objects, while 'symbolic' in some capacity are not clearly emblematic vs. arbitrary in nature. For example, the decoration of ostrich eggshells (OESs), possibly used as water carriers, may represent a form of shared esthetic or even symbol within a group, personal style or even emblematic style if water carriers are reasonably thought to be carried out there 'in the landscape of encounters' (Henshilwood and Marean, 2003; Texier et al., 2010, 2013; Henshilwood et al., 2014).

More clearly collective behavior exists in the evidence for the expansion of diet breadth, the transcendence of biogeographic barriers, and the expansion of the ecological niche, all of which point toward adaptability, flexibility, and the power to innovate specialist tools and/or behaviors which become relevant to a group or population (Kandel et al., 2016; Roberts and Stewart, 2018). Part of this expanded ecological niche may also include the control of landscapes and plant growth through controlled burning (Thompson et al., 2021). Further evidence for the understanding of the environment, innovation, and planning also comes from the seasonal exploitation of different resources (e.g., Steele and Álvarez-Fernández, 2011; Kyriacou et al., 2014).

Together, the aforementioned data have generally been used to support the theory that the capacity for complex culture emerged sometime with or after the earliest manifestations of *H. sapiens* morphology. However, there are several issues and caveats with this view that have appeared over the last two decades of research. The most obvious is that a good number of these traits can now also be linked to Neanderthals. For example, Neanderthals have now been found to have engaged in long-distance transport (Porraz and Negrino, 2008; Spinapolice, 2012; Doronicheva et al., 2019), buried their dead, structured their living spaces, and had increased diet breadth (Vaquero et al., 2001; Henry et al., 2014; Gabucio et al., 2018; Will et al., 2019b). Neanderthals also standardized their point forms in the Levant and clearly featured a diverse array of tool forms (see e.g., Groucutt, 2014). These discoveries somewhat problematize trait lists used for the MSA and undermined the idea of 'modern behavior' as something exclusive to *H. sapiens* (Zilhão, 2007; d'Errico and Stringer, 2011; Villa and Roebroeks, 2014). Does this mean there are no differences between the MSA record of *H. sapiens* and the Middle Paleolithic record of Neanderthals? On the contrary, there are differences in the intensities of manifested traits listed in Table 1, with examples of similar behaviors among *H. sapiens* being more widely expressed and more strongly manifested. Other behaviors, such as perforating shells, creating bow-and-arrow sets, and landscape-scale burning, are so far only known in the MSA, as opposed to the Neanderthal-associated Middle Paleolithic. These multifacetted and often gradual differences (see also Will et al., 2019b) suggest either a higher order cognition among *H. sapiens* or that the conditions for the expression of complex culture varied considerably between Neanderthals and *H. sapiens*, the reasons for which are currently unclear. Recent summaries of the archaeological and inferred cognitive differences between Neanderthals and modern humans have likewise argued for a middle position (Conard, 2015; Wynn et al., 2016).

A key point to make here, however, is that the variable expression of human cognitive capacity is linked not just to cognition itself but also to other factors such as demography, inherited (material) resources, anatomy, and environment—the interaction and feedback of which can lead to very different phenotypes (see e.g., Laland et al., 2000; Henshilwood and Marean, 2006; Hussain and Will, 2021). A second important point, harking back to the beginning of this section, is that the archaeological traits viewed as indicative of 'modernity' (expressed in the singular) are in fact reflective of collective behaviors rooted in cultural inheritance and group learning. The traits identified in the archaeological record are therefore one of many possible phenotypic expressions, as well as the expressions of various group behaviors—both of which are context-dependent.

Building on this, for both *H. sapiens* and large-brained hominins such as Neanderthals and Denisovans, complex behavior and culture can be viewed less as a real package but more as a general capacity, which is often underexpressed (Haidle, 2010, 2016; Haidle et al., 2015; Kandel et al., 2016). The important viewpoint proposed in these publications differentiates between empirically traceable behavioral performances and cognitive capacities that are theoretical constructs. In other words, behavior is about application, not ability, whereas cognition is about abilities, and not necessarily their application, which is context-dependent and relies on various demographic, social, and environmental aspects (see also Lahr and Foley, 1998). As an example, the focus on art and symbol as evidence for abstract thinking, theory of mind, language, and so forth, is understandable, but its lack does not necessarily reflect a lack of such human traits (see e.g., Henrich, 2004; Haidle, 2010, 2016). Unfortunately, only the reflections of behavior are directly observable, and much of the capacities available might remain unexpressed and archaeologically invisible. This raises the question as to whether the point where we see the various applications of complex cognition in the archaeological record is really the time when modern cognition *emerges*—particularly if strong parallels to the Neanderthal record exist.

If understanding complex cognition is not a black-and-white question but rather a matter of frequency, intensity, particular trajectories, historical contingencies, and interactions, are trait lists even useful? Or are trait lists encouraging the identification of the contents of modernity packages post hoc? As discussed, the traits listed in Table 1 can arguably provide meaningful links to (modern) behavioral and even cognitive complexity (e.g., Henshilwood and Marean, 2003; Haidle, 2010; Lombard and Haidle, 2012; Wadley, 2013, 2015) though they might be indicative of different aspects and expressions of it. On a pragmatic note, consideration of the traits linked to complex behaviors also allows for rapid assessment, permitting researchers to break down the record into directly observable, measurable, and quantifiable components of significance that play to the strengths of archaeology. As such, all archaeological assessments up to date have been based on some kind of (implicit or explicit) trait list and this is rooted in the very nature of our scientific discipline. However, which traits and archaeological finds are considered important may vary in much the same way as they do in paleoanthropological debates and traits have become much more complex, often consisting of multiple components (see Table 1). With that in mind, it is therefore the inferences based on such traits which are of central importance. For example, some traits were originally considered important in relation to the dominant theories of the time. Blades were once considered a key component of 'modernity,' simply because they were common in the Upper Paleolithic (Mellars, 1989, 1994; Straus, 1996). However, the production of blades can also relate to other factors, such as the need to maximize raw material volume, and it can be disputed whether blade making requires more planning depth than the production of recurrent Levallois flakes, for example (e.g., Muller et al., 2017, 2022). The argument that blades have special significance in view of their dominance in the Upper Paleolithic is therefore somewhat circular and indeed they are now recognized as a frequent element of MSA assemblages across Africa.

With these issues in mind, we review the state of knowledge on behavioral complexity in the MSA in different regions of Africa. We refrain from focusing on the presence or absence of singular classes of archaeological finds (e.g., art) or a categorical definition of 'cultural modernity' that refers to a predefined package of specific traits. Instead, we consider relevant empirical data in the form of diverse traits listed in Table 1 as heuristic devices that are variably manifested in the archaeological record and allow further inferences on various and distinct aspects that together make up human collective behavioral and cultural complexity. We follow a perspective that seeks to understand what these traits might refer to and the interactions of diverse variables that favor the processes expressing degrees of complex culture—and what this means for the emergence of 'modern human behavior.'

3. Reviewing the empirical evidence

3.1. Beginnings: Lithic technology of the Early/Middle Stone Age transition

At the root of both our species and previous thinking about a 'package' concept, is the MSA itself. The MSA, as defined by Goodwin (1928), follows the ESA (and Lower Paleolithic in Africa's neighboring regions) whose latest phases already begun to be marked by a greater degree of complexity and sophistication in lithic technology such as examples of Victoria West and 'proto'-Levallois cores (Raynal et al., 2010; Zaidner and Weinstein-Evron, 2016; Li et al., 2017). Unlike the ESA, the MSA lacks abundant large cutting tools and is focused on the production of flakes struck from prepared cores, some of which were subsequently retouched into a variety of forms not seen in the archaeological record before (e.g., Scerri and Spinapolice, 2019). The appearance of the MSA has been viewed as a profound shift in the conceptualization and manufacture of stone implements and the general behavioral capacities of its makers. Alongside the probable mounting of stone tips onto wooden hafts (Wilkins et al., 2012; Barham, 2013), the MSA itself marks the manifestations of consistently larger absolute and particularly relative brain size in the fossil record (Ruff et al., 1997; Rightmire, 2004; Shultz et al., 2012). This archaeological record shows intensified evidence for idiosyncratic variation of material culture restricted in both space and time associated with a higher tempo of technological change. This regional and temporal diversity (Clark, 1988; Barham, 2001) perhaps reflects the spread of an early *H. sapiens* metapopulation and a degree of adaptation to diverse environments (Scerri et al., 2018, 2019).

In the following presentation of empirical evidence, we pursue a geographically explicit approach considering that Africa as a single analytical unit masks the huge size of the continent as well as its enormous topographic, climatic, and environmental variability that was also relevant for the Pleistocene (see e.g., Lahr and Foley, 1998; Blome et al., 2012; Lahr and Foley, 2016). Recent paleoanthropological and genetic research has also suggested that instead of a single pan-mixing ancestral population of *H. sapiens* in the late Middle and Late Pleistocene, spatial and temporal structures existed (Gunz et al., 2009; Harvati et al., 2011; Lahr, 2016; Scerri et al., 2018; Bergström et al., 2021). While numerous divisions of the African continent are possible, we broadly follow the United Nations geoscheme (United Nations, 2019) splitting the continent into southern, eastern, northern, central, and western Africa. Although to a certain extent arbitrary when applied to the Pleistocene, this portioning has the advantages of being explicit, encompassing contiguous areas likely affected by similar climatic effects in the Pleistocene (Blome et al., 2012; Lahr and Foley, 2016), and following to a certain extent the research history of the MSA record. In a modern geographic and climatic sense, northern Africa is largely defined by the Saharan region; western Africa is bounded by the Sahara to the north and the central rainforests to the east; the Central African area is characterized by its rainforests; eastern Africa is defined by its highland regions and mosaic of different habitats, including lacustrine and fluvial corridors; and southern Africa is bounded by deserts and rainforests to the northwest and north-central and defined by its distinctive climate systems.

The transition to the MSA already features a degree of diversity in material culture that appears to be rooted in geographic distance. By the Middle Pleistocene, several changes are observed in the archaeological record. Previously, and for most of the Acheulean between ~1.8 and 0.3 Ma ago in Africa, assemblages are dominated by core tools and bifacial assemblages with wide geographic spread and comparatively little change over time. While patterns of regional typo-technological differentiation within Africa are not readily visible, some localized spatial structure and temporal changes, such as smaller and thinner handaxes with increased refinement and symmetry more often shaped by soft hammer percussion, have been observed in the Middle Pleistocene (Kuman, 2014; Lotter and Kuman, 2018; Schick and Toth, 2017). Based on this substrate, in North Africa, the transition from the ESA to the MSA sees bifacial tools becoming, on average, more symmetrical. Cleavers are rare and there is an increase in discoidal cores for the production of flakes (Raynal and Sbihi-Alaoui, 2009). Some of these flakes were retouched and turned into scrapers, notches, and denticulates, heralding the forms that would dominate the MSA (Raynal et al., 2001). By the late Acheulean, sites show evidence for an increased use of flakes from discoidal cores; ovate forms of handaxes made from flakes and cleavers become extremely rare (Raynal et al., 2001; Raynal and Sbihi-Alaoui, 2009). The end of the Acheulean goes beyond 200 ka at Cap Chatelier (Raynal et al., 2001), overlapping with the MSA to a significant degree. This assemblage is characterized by the production of predetermined flakes and small, thin bifaces, a diverse set of tools on flakes, and a very few cleavers. This Late Acheulean can even be defined as a transitional industry and was at one time thought to represent the technological reservoir from which the MSA emerged at Jebel Irhoud (Raynal et al., 2001), now known to date to ~315 ka (Richter et al., 2017).

In eastern Africa, the late or final Acheulean between ~500 and 200 ka is characterized by the selection of finer raw materials, more intense bifacial shaping with smaller, thinner, and more symmetrical handaxes, and the first occurrence of the Levallois method (Schick and Clark, 2000; Tryon et al., 2005; Gilbert et al., 2016). The earliest MSA is equally ancient as in northern Africa and dated to between 320 and 305 ka (Deino et al., 2018). Yet, Acheulean assemblages appear to have persisted contemporaneously in areas of eastern Africa into the end of the Middle Pleistocene, with handaxes and cleavers associated with Levallois flakes, points, and blades dating to 210 ka in Mieso (de la Torre et al., 2014) and surface finds of handaxes in the Upper Herto Member attributed to ~160 ka (White et al., 2003). Work in the Kapthurin Formation of Kenya found a complex pattern of handaxes interstratified with points and Levallois technology at various sites, suggesting both the contemporaneous use of various technologies and the origin of the earliest MSA technology present before 285 ka (Tryon and McBrearty, 2002; Tryon et al., 2005). Overall, the context of the emergence of the MSA in this region is comparable to that of North

Africa, and the technology is very similar, featuring prepared cores and retouched points (Brooks et al., 2018). At the same time, there are also differences in the frequencies of different tool types and retouch techniques that may reflect sample size differences or more profound regional traditions. For example, the early MSA at Olorgesailie and Kapthurin features blade cores as well as basal thinning on flakes and tools (Tryon et al., 2005; Brooks et al., 2018).

In southern Africa, sites from the period of the transition from the ESA to MSA are much less prevalent compared to the Late Pleistocene (Wurz, 2013; Wadley, 2015). The late Acheulean in the region sees the emergence of Victoria West cores (McNabb and Beaumont, 2012; Li et al., 2017) but is otherwise comparable to eastern and northern Africa. The so-called Fauresmith is a transitional industry between the ESA and MSA, somewhat poorly dated to ~500–300 ka and characterized by the presence of a low number of small handaxes, associated with Levallois-like cores, blades, and points (Herries, 2011; McNabb and Beaumont, 2012; Wilkins and Chazan, 2012; Kuman et al., 2020). The last large cutting tools in southern Africa appeared at the end of the Middle Pleistocene at Duinefontein (Klein et al., 1999). Interestingly, the site of Kathu Pan has evidence for the manufacture of blade technology, hafted stone points, and pigments potentially dating to ~500–300 ka (Wilkins et al., 2012; Watts et al., 2016), but the ages are controversial and not unanimously accepted.

Less is known about the transition to the MSA in western and central Africa. ESA artifacts have been documented in different ecological zones (e.g., Braucher et al., 2022), highlighting a need to document evolutionary processes in tropical forests, that may have included refugia suitable for hominins (Blinkhorn et al., 2022; Scerri et al., 2022). 'Transitional' ESA to MSA industries have not yet been reported, although this is likely to change with the increased focus on these less well-documented regions. Certainly, Middle Pleistocene MSA dates are now known for both western and central Africa (Barham, 2000, 2002; Clark, 2001; Soriano et al., 2010; Niang et al., 2018; Braucher et al., 2022).

While the transition to the MSA represents a profound shift, it is also clearly rooted in the increasing sophistication and complexity of the Late Acheulean and indeed overlapped with it in various African regions. These advances soften the concept of an MSA 'revolution' and emphasize a complex pattern of the Late Acheulean/early MSA transition, both of whose makers may well have been the earliest *H. sapiens*. This pattern of complex overlapping at the end of the Acheulean might even be a global phenomenon (Key et al., 2021).

3.2. Developments: Lithic technology of the Middle Stone Age during the late Middle and Late Pleistocene

The early MSA in Africa does not substantially change in the following millennia but becomes the substrate upon which other behaviors and technologies build. In North Africa, early MSA sites such as Jebel Irhoud (~300 ka), Benzú Cave (~250 ka), Sai Island Site 8-B-11 and Kharga Oasis (both ~220 ka), and Ifri n'Ammar (~170 ka) are variable but predominantly flake-based, with an emphasis on local raw materials, Levallois and/or discoidal technology, high proportions of scrapers, points, and denticulates, and in some cases rare heavy-duty implements such as core-axes (Van Peer et al., 2003; Nami and Moser, 2010; Ramos-Munoz et al., 2016; Richter et al., 2017). The subsequent innovation of stemmed ('pedunculated'/'tanged') Aterian tools broadly emerges with the Last Interglacial around 130 ka (Richter et al., 2010; Doerschner et al., 2016; Campmas, 2018). Many classic MSA forms are manufactured with basal stems or tangs, from points to side and end retouched tools, alongside other basal alterations such as thinning (Scerri, 2013a, 2013b, 2017a). In addition to this, other basal modifications such as thinning and shouldering mark a general intensive concern with hafting (Rots et al., 2011; Scerri et al., 2014; Tomasso and Rots, 2018). Tanged tool assemblages also have an enormous spread broadly corresponding to the modern extent of the Sahara and the North African littoral and hinterland regions, but they are completely absent elsewhere (Scerri, 2012, 2013a, 2017a). Beyond the Western Desert and the Nile, other MSA assemblage forms dominate. In addition to purely technological changes, the Aterian or tanged tool assemblages also feature the long-distance transport of exotic raw materials (Clark et al., 2008), possible pressure flaking, and small points that may indicate the presence of bow and arrow technology (Scerri, 2017a).

In eastern Africa, MSA lithic technology shows a patchwork of variation through time and space, with variability often emphasized as a key component, despite long periods of relative homogeneity also being evident (Shea, 2008; Tryon and Faith, 2013; Lahr and Foley, 2016; Blinkhorn and Grove, 2018). While research has shown a general decline in the average size of points over time (Tryon and Faith, 2013), there are no formally defined temporally or regionally specific 'diagnostic tools.' Nothing is comparable to the close-by Aterian in the north and northwest, with the possible exception of 'tranchet-shaped points' from Gademotta and Kulkuletti (Douze and Delagnes, 2016; but see Sahle and Braun, 2018; Douze et al., 2018). Long-distance transport of lithic raw materials has been intensely studied in eastern Africa due to the telltale geochemical signatures of obsidian outcrops. Site-to-source transport distances for obsidian of >50 km are already known by the earliest MSA of the region, increasing later to distances up to around 200 km (Negash et al., 2011; Blegen et al., 2018; Brooks et al., 2018). A characteristic feature of the eastern African MSA is the variable presence of bifacial points, which occur in the region from most sites and spanning the late Middle Pleistocene until the beginning of the Holocene (e.g., Tryon and Faith, 2013; Blinkhorn and Grove, 2018). Some of the earliest MSA points of the region have been interpreted as systematic tranchet removals (Douze and Delagnes, 2016) or as projectiles delivered at high velocity as the tip of spears (Sahle et al., 2013; but see Douze et al., 2018). No indications of bow and arrow technology have yet been presented for this region, although it seems probable that such evidence will be uncovered in the future. Unlike other regions of Africa, an early potential transition from the MSA to LSA might appear already by 71 ka (Shipton et al., 2018) or more frequently observed around 50–40 ka (Ambrose, 1998; Miller and Willoughby, 2014; Tryon et al., 2018) depending on the definitions used for these periods. In any case, an increase in small, backed pieces and diversification in nonlithic material culture characterizes the MSA from Marine Isotopic Stage (MIS) 3 more generally in this region and is worth mentioning here due to the early dates which are well within a classic MSA time frame elsewhere in Africa.

In southern Africa, Middle Pleistocene MSA occurrences without Acheulean elements called 'early MSA' date between 280 and 130 ka. They are quite variable but mostly encompass flake-based assemblages with few retouched forms and a focus on local raw materials, though some sites feature large blades and bifacial points (Lombard and Haidle, 2012; Wurz, 2013; Schmid et al., 2016; Chazan et al., 2020). The oldest of these assemblages at Florisbad (~280 ka) is of similar age as the cranium from the same site, which some researchers interpret as an early *H. sapiens* (e.g., Grün and Beaumont, 2001; Kuman et al., 2020). Suggestions that some of these early MSA tools in southern Africa might have been produced by the recently discovered remains of *Homo naledi* (Berger et al., 2017) remain speculations as these fossils are so far not associated with any lithic artifacts. The Late Pleistocene archaeological record (~120–30 ka) reveals a marked increase in sites and artifact density with a higher tempo of technological change, forming the basis of numerous technocomplexes separated mostly in time and sometimes in space (Wurz, 2013; Wadley, 2015; Will et al., 2019a). From MIS 5 onwards, lithic assemblages bear frequent evidence for the manufacture of large, standardized blades sometimes produced by soft and organic hammers (Wurz, 2002; Will et al., 2014; Schmid et al., 2019), backed pieces and bladelets (Lombard, 2009; Brown et al., 2012; de la Peña, 2015; Blessing et al., in press), and carefully shaped unifacial and bifacial points with different regional and temporal expressions (Villa et al., 2009; Conard et al., 2012; Porraz et al., 2013; Archer et al., 2016; Will and Conard, 2018; Bader et al., 2022), the latter also manufactured by pressure flaking (Mourre et al., 2010; Rots et al., 2017). Small, backed pieces and their hafting traces have been interpreted as reflecting the origin of bow and arrow technology already at ~60 ka (Lombard and Phillipson, 2010). MSA people produced compound adhesives, often featuring both ochre and plant material, for their use in composite implements and weapons (Lombard 2006; Wadley et al., 2009). Frequent import and use of nonlocal raw materials of high quality, and potentially other natural materials (Wilkins et al., 2021) is a phenomenon covering much of the Late Pleistocene (Will and Mackay, 2017), with distances up to >200 km for silcrete in Botswana (Nash et al., 2013, 2016). There is also abundant evidence for the heat treatment of silcrete beginning in MIS 6 and continuing through until MIS 3 (Brown et al., 2009; Schmidt et al., 2013; Schmidt and Mackay, 2016).

While still heavily understudied, some new data have emerged from central and western Africa since 2000 that provide key reference points in poorly understood regions. In central Africa, the MSA archaeology of the late Middle Pleistocene features both bifacial shaping of finely made large lanceolate points and the manufacture of small backed pieces in central Africa within a Lupemban context (earliest ages currently coarsely estimated to be ~270–170 ka at Twin Rivers and Kalambo Falls; e.g., Barham, 2000, 2002; Clark, 2001; Taylor, 2022). Long-distance transport of stone tools is rare but documented at Mumbwa Caves up to 200 km during MIS 5e (Barham, 2000). During MIS 4, there is again some evidence for the presence of bifacial lanceolate points in central Africa.

Novel data surfacing from western Africa demonstrate that this region features a long duration of the MSA from the end of the Middle Pleistocene all the way until the Terminal Pleistocene/Holocene boundary, persisting alongside penecontemporaneous LSA assemblages (e.g., in Senegal until ~12 ka; Chevrier et al., 2016; Scerri et al., 2017, 2021). Relatively well-studied sites in western Africa (i.e., in Senegal) yield both a temporal signal of high variability regarding both core reduction and tool assemblages with rapid rates of change (Robert et al., 2003; Scerri, 2017b; Chevrier et al., 2018), as well as areas of longer-term stability (Niang et al., 2020). From MIS 5, crudely shaped bifacial tools have been found together with more typical MSA forms, including scrapers and notches (Douze et al., 2021). Other types of small bifacial foliate points are known from western Africa, but only in pulses during MIS 4–2 (Scerri, 2017b; Chevrier et al., 2018; Scerri et al., 2021), with some evidence for their production via pressure flaking at least from one site (Schmid et al., 2022).

3.3. Indicators for ecological flexibility and social complexity: Nonlithic archaeological material from the Middle Stone Age

As can be seen from the aforementioned summary, the MSA, as defined by its (lithic) technology, features a number of changes that cover a gamut of complex behaviors, many of which already made the ‘trait lists’ and packages used for charting ‘modern human behavior’ in the Upper Paleolithic in the 1990s (Mellars, 1989, 1994; Mellars and Stringer, 1989) before being identified in the MSA (McBrearty and Brooks, 2000). New innovations have also been identified since then, including heat treatment, pressure flaking, hafting styles, novel tool forms, and complex armatures, which all speak to planning, memory, cooperation, forms of communication, and task specialization, since they all require a series of stages of manufacture that also involve the use of different materials and treatments (see Table 1; Scerri, 2013b; Schmidt and Mackay, 2016; Rots et al., 2017). The long-distance transport of raw materials might also imply the presence of some type of exchange network and perhaps even concepts of value, esthetics, and ritual. The value of stone tools in particular lies in their abundance, demonstrating that such complex behaviors were relatively widespread. Significantly, these MSA assemblages are also associated with other nonlithic remains that attest to complex behaviors not observed previously, which we will discuss in relation to notions of ecological flexibility and social complexity (see Table 1).

Archaeological work since 2000 has uncovered substantial evidence that the MSA features a novel degree of flexibility in subsistence, diet breadth, and the types of occupied ecological niches. From the early MSA, there is evidence for plant processing through grinding (Van Peer et al., 2003) and the exploitation of diverse resources. The latter ranged from the intensified occupation of coastal landscapes and exploitation of marine resources in both northern and southern Africa (summarized in Will et al., 2019b) to a broad range of prey animals, including large and dangerous species marking MSA people as capable, sophisticated hunters (Faith, 2008; Dusseldorp, 2010; Clark and Kandel, 2013). Plant use is more widespread in the MSA than previously believed, with the exceptionally well-preserved record from southern Africa demonstrating the dietary use of grass seeds (Mercader, 2009), cooking and consumption of geophytes (Wadley et al., 2020a), and the use of sedges for bedding and as insect repellents by 200 ka, and continuing well into the Late Pleistocene (Goldberg et al., 2009; Wadley et al., 2011, 2020b; Sievers et al., 2022). New raw materials also become more frequently incorporated into people's technological repertoire. Various types of formal bone tools occur for the first time in northern and southern Africa as part of new hunting weapons but also domestic tools (Henshilwood et al., 2001; Backwell et al., 2008; d'Errico et al., 2012; Stoetzel et al., 2014; Campmas, 2018), with some being linked to the removal of fur in potential clothes making (Hallett et al., 2021).

MSA sites also have a much broader distribution than ESA sites and are not tethered to water sources (Basell, 2008), as highlighted by McBrearty and Brooks (2000). The discovery in southern Africa of decorated ostrich eggs has been argued to indicate the presence of water storage technology that may partly explain differences in the spatial patterning of sites, at least in the Late Pleistocene (Texier et al., 2010, 2013; see also Mackay et al., 2022). The decoration of practical objects like water carriers also points to a coevolution and fusion of the mundane and the symbolic, an aspect that has been less well considered. This notwithstanding, increased diet breadth and the colonization of diverse environments, from islands to lowland tropical forests is described as one of the signatures of modern behavior (McBrearty and Brooks, 2000). Recent finds extend this ecological flexibility to high-altitude environments (Ossendorf et al., 2019) and are generally being characterized as the manifestations of a ‘generalist specialist niche’ specific to humans (Roberts and Stewart, 2018). Such niche expansion and environmental versatility have also been documented quantitatively for the southern African MSA (Kandel et al., 2016; Lombard, 2016; d'Errico et al., 2017). Other behaviors attest to the attempts to control and modify environments as well as adapt to them. There is evidence of widespread burning in Malawi from around 90 ka, influencing vegetation composition, controlling wildfire outbreaks, and perhaps modifying hunter-gatherer returns (Thompson et al., 2021). Another instance of widespread niche construction concerns the generation of artificial landscapes made up of the long-term procurement, knapping, and transport of lithic material, known from open-air MSA contexts (Foley and Lahr, 2015; Braun et al., 2021). Such materially enriched landscapes acted as external raw material reservoirs for groups of mobile hunter-gatherers and entrenched their own position in the wider coordinate system of land use through repeated hominin visits and material input over time (Hussain and Will, 2021). The same argument of an increasingly 'cultured' landscape can be made for focal loci in landscapes such as rock shelters and caves with their cumulative build-up of knapped rocks. Mining activities known at least by 100 ka for chert in Egypt (van Peer et al., 2010) and by >30 ka for ochre (Bader et al., 2021) further attest to the capabilities of MSA humans to be the cause of permanent to semipermanent changes in landscapes.

Social complexity is now likewise evident from several independent lines of evidence. MSA assemblages are associated with both naturally and intentionally perforated marine shells that may represent personal ornaments (Steele et al., 2019) and shared social norms based on the specific ways of their manufacture (d'Errico et al., 2005; Vanhaeren et al., 2013). Perforated marine shells are particularly abundant in the northern African MSA, deriving from a total of nine sites between ~140 and 80 ka with a preference for *Nassarius* shells (Bouzouggar et al., 2007; d'Errico et al., 2009; Nami and Moser, 2010; Dibble et al., 2012; Stoetzel et al., 2014; Sehasseh et al., 2021). In southern Africa, MSA shell beads have so far been found only in MIS 4 (Will et al., 2019b). The earliest and single case for marine shell beads (*Conus* sp.) in eastern Africa comes from Panga ya Saidi at ~67–63 ka (Shipton et al., 2018). What is certain is that these perforated shells were collected and transported far from the coast, indicating local exchange networks focused on something other than exotic stone (Henshilwood et al., 2004; d'Errico et al., 2005, 2009; Vanhaeren et al., 2006). MSA people also used other raw materials for bead making, with particular frequent beads of OES in the MSA of eastern Africa beginning by ~50 ka (Miller and Willoughby, 2014; Tryon et al., 2018; Miller and Wang, 2022), with lower numbers and examples of drilled bones reported from MIS 3 contexts in southern Africa (e.g., Steele et al., 2016). Similar ways of manufacture and variability in OES bead forms speak to both a connection to social groups and exchange between people (Stewart et al., 2020; Miller and Wang, 2022).

The collection and use of pigments has been reported from a large number of sites across Africa (Fig. 1), starting already between 320 and 200 ka in central and eastern Africa (Clark, 2001; Barham, 2002; Brooks et al., 2018), and ochre processing is very frequent in the Late Pleistocene of the latter region (Rosso et al., 2016; Shipton et al., 2018; Tryon et al., 2018; see Dapschauskas et al., 2022 for a pan-African overview). Northern Africa shows the use of yellow and red pigments at Sai Island by ~200 ka (Van Peer et al., 2003) but more frequently in MIS 5 (Nami and Moser, 2010; Barton and d'Errico, 2012; Campmas, 2018). In southern Africa, there is patchy evidence for pigment use in MIS 8–7, increasing in MIS 6 and much more frequently as a continuous behavior in MIS 5–3 (Watts, 2010; Watts et al., 2016; Hodgskiss, 2012; Dayet et al., 2013; Wadley, 2015). The use of pigments is linked to other lines of evidence indicating art or ritual, such as ochre crayon 'drawings' and etched designs from Blombos Cave (Henshilwood et al., 2009, 2018), as part of two ochre-processing kits at ~100 ka for the production of paint (Henshilwood et al., 2011) and as the only evidence of parietal art from the MSA from Apollo 11 in the form of a painted slab dated to ~30 ka (Vogelsang et al., 2010). Similar patterns of abstract designs on engraved OES from sites >300 km distant in South Africa at Diepkloof (Texier et al., 2010, 2013) and Klipdrift Shelter (Henshilwood et al., 2014) suggest the existence of long-range connections and communication systems during MIS 5/4. A similar practice of linear engravings on OES fragments was discovered at Goda Buticha (~43–34 ka; Assefa et al., 2018). While rare, the oldest known human burials with evidence for the digging of pits and supplemented with grave goods come from Border Cave (d'Errico and Backwell, 2016) and Panga ya Saidi (Martinón-Torres et al., 2021) that likely indicate coping mechanisms for grief, shared group values, and potentially even belief systems. Linked to this phenomenon are the abundant *H. sapiens* burials from the Levant dating to as early as ~120 ka, generally regarded as a population of African migrants (Groucutt et al., 2019).

Social boundaries and aggregations may also be manifested in the available data. For example, Aterian tanged tool assemblage types common in different regions of North Africa are found together at a site in the central Sahara, with all the examples of these elaborate tool types (i.e., foliates, points) made on the same exotic raw material (Scerri et al., 2014). The bounded geographic nature of the Aterian and the fact that it does not appear to cross the major rivers may also partly be explained through cultural or social choices and constraints, although this is much harder to demonstrate. Some of the spatiotemporal patterning of idiosyncratic lithic artifacts among the technocomplexes in the southern African MSA might also delineate bounded groups with ongoing social exchange of information (Högberg and Lombard, 2020; Way et al., 2022). In a study of strontium isotope analyses of OES beads, Stewart et al. (2020) were able to identify their long-distance exchange, indicating the existence of macroscale, transbiome social networks over many hundreds of square kilometers in southeastern Africa that stretch back to the later MSA at ~33 ka. A more recent study from eastern and southern Africa may confirm the existence of such large-scale social networks, with eggshell bead technology spreading from its likely origin in eastern Africa southward approximately 50–33 ka (Miller and Wang, 2022).

In sum, our review of empirical data from the MSA since 2000 provides a wide range of new evidence from lithic and nonlithic material culture that match with and add to McBrearty and Brooks' (2000) 'signatures of modern behavior' (see also Table 1). These traits allow inferences on ecological flexibility, symbolic behavior, economic and social organization, technological innovation, and standardization of early *H. sapiens* and are likely in part—though not comprehensively—due to an underlying increase in cognitive capacities. New data strengthen the claim for an African origin of many of these traits and have provided novel innovations that also originated in the MSA in different regions, such as abstract engravings, plant beddings, heat treatment, or compound adhesives. In the next section, we discuss new perspectives about how the current empirical data can best be viewed and interpreted to understand the patterns of cultural evolution in early *H. sapiens*.

4. Patterns in the record: Inferring a complex mosaic of cultural evolution in the Middle Stone Age

As discussed above, the dominant model for the origins of modern behavior shifted from a revolution to a gradualistic model, in which 'stepwise' (McBrearty and Brooks, 2000) changes in the archaeological record were related to ideas of a ratchet effect, or ideas of cumulative culture for the evolution behavioral complexity in *H. sapiens*. But does this gradualistic aspect of the model fit the empirical evidence as reviewed above? At the root of the discussion of a gradualistic emergence of behavioral complexity is the MSA itself. Historically, the MSA was defined on purely lithic terms and inserted as a third period between the already existing classifications of the ESA and LSA. The technology of the MSA was neither ESA nor LSA, such as lacking in handaxes and other large core tools of the former and microliths of the latter (Goodwin 1928; Goodwin and van Riet Lowe, 1929). Defined in part on what it was not, attempts

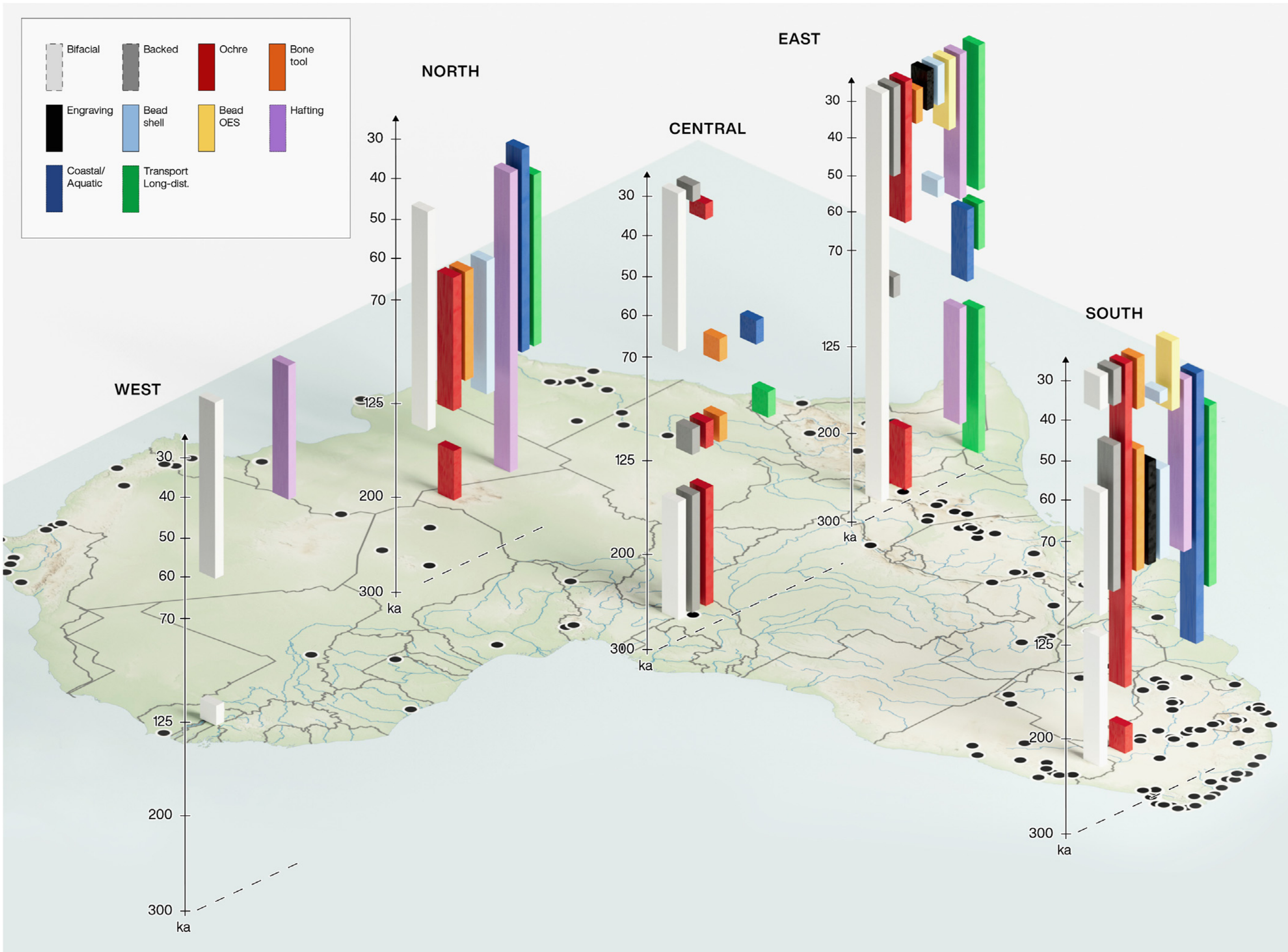

Figure 1. Map illustrating the distribution of stratified Middle Stone Age (MSA) sites from the 'ROCEEH - Out of Africa database' (www.roceeh.net) and a summary diagram for the appearance and timing of selected elements of complex material culture and behavioral innovations during the MSA from ~300 to 30 ka by the different regions (this is a subset of traits from Table 1 excluding additional aspects such as burials, heat treatment, or increased diet breadth for reasons of comprehensibility). Note the divergent trajectories between different parts of the African continent.

to characterize the MSA more positively included traits such as flake-based industries with the appearance of facetted and convergent flakes, with various smaller-sized tool types—particularly unifacial and bifacial points—made on these flakes (Goodwin and van Riet Lowe, 1929; Clark, 1959; Klein, 1970). Today, the hallmark of the MSA consists of the production of various blanks with predetermined size and shape from prepared cores, such as the Levallois method (e.g., Clark, 1982, 1988; Wurz, 2014). With much ongoing and enduring criticism concerning high-level classificatory units and their many problems (e.g., Clark et al., 1966; Clark and Kleindienst, 2001), most prehistorians today use the MSA as a descriptive shorthand for a temporal stage to describe assemblages of the late Middle and Late Pleistocene, loosely associated with the lithic definitions before. The classification and assessment of the MSA is further confounded by general differences observed between the MSA prior to the Late Pleistocene and after this point. Broadly speaking, after the Last Interglacial, the MSA substrate becomes much more enriched and varied by the appearance (and disappearance) of different tool types and methods of lithic manufacture alongside nonlithic elements like shell beads and decorated OESs, as discussed above (e.g., Tryon et al., 2005; Tryon and Faith, 2013; Wurz, 2013, 2014; Wadley, 2015). Yet, as shown by our review of empirical evidence above, any simplistic dividing of the MSA into two distinct phases is also belied by the pace of change, sharp regional variation, and very long periods of stasis that speak to a surprising lack of cumulative culture.

Reviews such as McBrearty and Brooks (2000), as well as many others, emerged from a context that had previously seen a human revolution in the European Paleolithic. They therefore understandably tend to focus on the appearance of novel features within the MSA archaeological record over time—and less on their disappearance or overall geographical spread—and often treat Africa as a unit of analysis, which is not a coherent biogeographical reality (with, e.g., northeast Africa having more in common with the Arabian Peninsula than southern Africa). The picture changes when we begin to break down this unit of analysis but also look at more stable components of the record. For example, it is also true that the generic lithic elements of the MSA that first emerged around ~300 ka continue, seemingly unchanged, for many thousands of years (Scerri et al., 2017, 2021; Thompson et al., 2018), which may suggest that such artifacts are not a particularly useful reflection of cognitive capacity. Yet it may also point to the base-level manifestation that a major cognitive shift allowed, with subsequent developments based on a cultural, rather than a biological scaffold. When looking at different regions of Africa on a continental scale, the MSA record appears to be peppered with the appearance, disappearance, and reinvention of key technological and social innovations alongside the extraordinary long persistence of the mundane and the unchanging (Fig. 1). At no point, until the LSA (or Upper Paleolithic), is there a substantial, long-term, sustained cumulative change, and even parts of the LSA record retain a mosaic-like structure (e.g., Shipton et al., 2018). Does this tally with a 'gradualistic view,' and can behavior be truly 'modern' if the only examples of cumulative culture are temporally and spatially discrete, and characterized by unimaginably long periods of stasis (Tennie et al., 2009)?

Our review presented here (see also Scerri et al., 2018; Will et al., 2019a) indicates that the temporal pattern of technological change during the African MSA is more complicated than being one of mostly gradual accumulation or incremental assembly (sensu McBrearty and Brooks, 2000: 529–531) across Africa. Whereas McBrearty and Brooks (2000) initially formulated the expectation that a gradual process need not imply a unidirectional trajectory that unfolds similarly in each region, they did not take an explicit spatial approach in the presentation of their results because much of the data available today was simply not yet discovered. There has been an exponential increase of MSA studies with a trove of new discoveries since 2000—particularly in regard to nonlithic material culture—coupled with advances in chronometric controls of findings in methods such as OSL, TL, ESR, and U-Series that have also provided a much different temporal perspective. As a result, differences between their findings and ours appear to largely stem from a combination of higher quantity and resolution of archaeological finds and the diverse ways of presenting said data.

A useful analytical strategy for gaining a higher resolution of patterns of cultural evolution in the MSA breaks down Africa into different analytical regions, recording the temporal patterns of the presence and absence of different selected traits in each as done here (see also Scerri et al., 2018; Will et al., 2019a). The resulting pattern of this approach shows that the presence, abundance, timing, and duration of many innovations are often asynchronous across regions, which can be best characterized as a complex mosaic (Fig. 1). Multiple pathways of cultural change occur in different African regions and we found no pan-African trajectory for the cultural evolution of *H. sapiens*. Rather than a gradual or linear accumulation of complex material culture, different African regions show a mix of continuous and discontinuous traits indicative of behavioral complexity—sometimes even within smaller areas such as southern Africa—and a patchwork of technologies. Instead of a continent-wide, directional and unilinear models of cultural change, these data suggest more highly contextualized, temporally variable, and historically contingent trajectories in different regions, which one of us has previously discussed under the concept of 'complex landscapes of cultural evolution' (Will et al., 2019a). Enduring behaviors underlying these patterns can be found particularly in lithic technology and subsistence, whereas nonlithic material culture is much more variable and prone to flickering. Our observations match well with previous research stating that what is often considered an MSA 'package' in Africa is rather an asynchronous appearance of characteristics, regional contrasts, and a lack of simple cumulation on a common substrate (Lahr and Foley, 2016; Spinapolice, 2020). Instead, what does unite much of Africa are the generic components of the MSA, an early onset for some innovations close to the beginning of the MSA such as pigment use, hafting or long-distance transport of materials, and a general (non-linear) increase in the dynamics of the appearance (and subsequent disappearance) of complex material culture with the onset of the Late Pleistocene.

Based on current data, the manifestations of human cognitive capacities attested to by examples of behavioral complexity are certainly polycentric (Conard, 2005, 2008, 2015; Scerri et al., 2018; Will et al., 2019a). Considering this mounting material evidence from Africa, the period 300–30 ka can best be characterized by multiple, temporally variable, and nonlinear trajectories in different regions. Elements of this model fit with recent theoretical developments which reject 'revolution' narratives but also scenarios of strictly gradual and linear trajectories of cultural evolution for early *H. sapiens*. Such concepts favor nondirectional patterns of cultural change with a focus on historical contingency, cognitive capacities, behavioral flexibility, environmental context, and path dependence (Kuhn, 2006; d'Errico and Stringer, 2011; Lombard, 2012; d'Errico and Banks, 2013; Haidle et al., 2015; Kandel et al., 2016; Lahr and Foley, 2016; Wadley, 2021). The complex patterns for cultural evolution are seemingly complemented by observations long made by paleoanthropologists who argued for a pan-African spread of modern morphological traits (Hublin, 1992; Stringer, 2002; Gunz et al., 2009). However, the patterning of the cultural data in Africa appears to be both nonlinear as well as more patchy, rather than a gradual scaffold upon which new innovations can cumulatively build. For example, there seems to be little to no persistence of the major cultural innovations of the MSA, indicating that the accumulation of innovations is not stable over long periods. Indeed, many innovations are reinvented in different places at different times, such as diverse hafting modifications or the manufacture of shell beads. Even within periods of cultural efflorescence, such as the Aterian in North Africa, there is significant stasis after the initial period of innovation during MIS 5 (Scerri, 2017a).

The pattern described above can best be visualized via an analogy to the concept of fitness landscapes coming from the biological sciences. Viewing behavioral, cultural, and cognitive performances as complex, multidimensional fitness landscapes draws on S. Wright's (1932, 1982) work on biological systems. His complex landscapes feature several adaptive peaks and valleys of different heights, corresponding to local fitness maxima and minima. Recently, archaeologists have adopted this concept with different peaks standing for higher behavioral complexity as the result of diverse influences (Kuhn, 2006; Lombard, 2012, 2016; Will et al., 2019a). This approach maintains that patterns of cultural evolution are spatially susceptible, affected by multiple factors, and historically contingent on the initial conditions of populations (path dependence). When applied to the African MSA, adding separate populations in different regions to a 'continent-wide' fitness landscape affected by specific geological, social, environmental, biological, and demographic factors will create highly complex spatial topographies. Based on this topography alone, single, optimal, and stable pan-African adaptations reflected in comparable material culture should be the exception. During most time, early modern humans were confronted with a multitude of local, suboptimal fitness states varying dynamically by region. Temporal change was often asynchronous over the continent due to different external or internal stimuli. Rarer periods during which factors acted in a similar way on different regions might result in broadly comparable solutions and similar patterns of cultural change. Information transmission between connected groups may also serve as attractors to reach similar adaptive peaks that result in more homogeneous signals of cultural change within regions. Concurrently, this situation creates more divergence at the boundaries of populations or social networks, based on the assumption of population substructure on larger spatial scales. Differences in the trajectory between regions can also be amplified by inertia effects, with the differential accumulation of past material solutions constraining and shaping the paths of subsequent decisions.

The complex patterns for our cultural evolution presented above to a certain extent mirror the patterning of derived morphological traits. At the beginning of the MSA, these anatomical characteristics also evolve in a mosaiclike pattern until some point between 100 and 40 ka when the constellation of traits that defines contemporary populations begins to be found in single individuals (Gunz et al., 2009; Lahr, 2016; Scerri et al., 2018). Primitive morphological traits also persist to the terminal Pleistocene (Harvati et al., 2011), much like the persistence of a classic MSA to the Holocene transition (Scerri et al., 2021). At the same time, the relationship between morphology and cognition seems to decouple after the initial emergence of *H. sapiens* going along with an increasing autonomy from selective pressures of the immediate environment. Higher emphasis on cultural and other extrasomatic means of environmental mediation becomes manifest in the exponential increase of behavioral options, more frequent niche construction, and a mismatch between environmental and cultural change at times is already observed in the MSA (Clark, 2013; Porraz et al., 2013; Conard and Will, 2015; Tryon and Faith, 2016; Hussain and Will, 2021). This process culminates in the capacity to react in a seemingly endless host of different social, economic, and technological ways to particular environmental circumstances, marking the behavioral 'hyperplasticity' and cultural diversity seen in today's humans (e.g., Conard, 2015).

If 'gradual' implies strict accumulation in a linear fashion through time, this is not something that is supported in the MSA archaeological record, despite the clear cognitive capacity for it. Instead, we see a saw tooth pattern of innovation, stasis, and loss over an MSA substrate, manifested in different ways and at different times. When projected onto space and time across the African continent, this patterning takes a mosaic-like appearance of a complex landscape (Fig. 1). What explains this patterning?

5. Causes and mechanisms of change

So far, the drivers of behavioral change that underlie the cultural evolution of modern humans have been left aside for the most part in this contribution. Models emerging in the last 20 years have variously cited environmental and climate change (McCall, 2007; Ziegler et al., 2013; Mackay et al., 2022), dietary factors (Parkington, 2001, 2010; Marean, 2010, 2014), cognitive changes (Deacon and Wurz, 2001; Wynn and Coolidge, 2008) potentially caused by genetic mutations (Klein, 1994, 2000; Klein and Edgar, 2002), and changes in demography, communication networks, and social structures (Lahr and Foley, 1998; Jacobs et al., 2008; Powell et al., 2009; Sealy, 2016; Tryon and Faith, 2016) as potential causes. The most prominent explanations that account for the patterning of the MSA in the past generation while acknowledging its links with behavioral complexity are typically split between a more biology-based cognitive framework and a demographic view focused on population size and spatial distributions.

5.1. Behavioral complexity and changes in the human brain

The biology-based cognitive framework views the capacity for complex behavior as something that occurred after speciation, along our trajectory of evolution, caused by some form of a heritable biological change (Mithen, 1996; Klein, 2000). This is usually framed in terms of a neural mutation that gave rise to greater cognitive complexity (Klein, 1994, 2000, 2009). In such models, there is usually an abrupt change with a clear difference of before and after, allowing for a clear point in time to be discerned at which humans are behaviorally 'modern.' According to Klein (1994, 2000, 2009), a sudden origin of behavioral modernity within Africa occurred at a late point around ~50–40 ka, exclusive to modern humans. It is initiated by a genetic mutation that caused neurological changes in the brain (e.g., linguistic capacities), which prompted a flourishing of behavioral innovations seen in the MSA/LSA transition in Africa that is then exported to Eurasia.

While the model has been very influential as seen by frequent citations inside and particularly outside of the field (e.g., Harari, 2014), there are various issues associated with it. For one, by the timing proposed at 50–40 ka, modern humans had already split into separate populations, meaning that either this mutation occurred independently in different modern human lineages, or that there was a rise to substantial frequencies after human populations had dispersed out of Africa with further world colonization wave by individuals bearing the mutation, for which we have no evidence. At least as important, recent studies looking for such traces found neither neurological nor genetic bases for a revolutionary change in the human genome taking place during MIS 3 (Mallick et al., 2016; Neubauer et al., 2018). Finally, the pattern of cultural innovations manifested in the MSA archaeological record presented here negates the model. The MSA records show a suite of innovations starting already around its beginning without a clear break or revolution visible at a specific point. Instead, various complex behaviors can be traced back far in time and were (re-) invented in various areas at various points in time (e.g., bead working, bone tools, or abstract signs).

Other scholars have argued that at the beginning of the MSA and with the origins of the *H. sapiens* phenotype, the basic cognition of our species was already in place (e.g., Lahr and Foley, 1998; Marean, 2011; Shea, 2011). In such a scenario, the large (relative) brain size increases observed in the late Middle Pleistocene and with the origin of our species laid the groundwork for the behaviors typically seen today. Yet again, a direct causality of changes in the human brain and cognition alone falls short as we do not observe an exponential increase or 'revolution' in behavioral complexity in the archaeological record around ~300 ka (at least not to the levels seen in the Late Pleistocene; see also Wadley, 2021). What might explain this disparity is the distinction between the capacities for complex behaviors that originated with the origin of our species from the application of such, which might have needed other factors on top to be fully expressed (see below). Other approaches linking the human brain to behavioral complexity have also been discussed. Instead of mere absolute or relative brain size, changes in brain ontogeny, organization, and neural connectivity might be more important (e.g., Gunz et al., 2009; Hublin et al., 2015; Logan et al., 2018; Neubauer et al., 2018; Bruner, 2021; Zollikofer et al., 2022) and a way for future studies in this regard. Tracing some of these changes is, however, challenging and reliant on a small sample of relevant fossil crania, as is relating them to the pattern seen here.

5.2. Behavioral complexity and human demography

Recently emerging models have suggested that the behavioral and biological mosaic seen in human evolution might be in small or large parts an outcome of demography and overall metapopulation size. McBrearty and Brooks (2000: 532–533) already discussed the potential impact of population size and density on the MSA/LSA transition and highlighted the fact that the MSA has a much wider distribution than the Acheulean, and that preservation bias alone is unlikely to explain this. From a general theoretical perspective, demographic aspects, including population structure, density, and interconnectivity, but also the variable pathways of cultural transmission, constitute key variables to explain patterns of recent cultural change, such as the appearance and disappearance of cultural variants, and their differential uptake and dispersion (Cavalli-Sforza and Feldman, 1981; Henrich, 2001; Richerson and Boyd, 2005). Mathematical models on the relationship between demographical variables and cultural complexity have reported a positive effect of increasing population size and social interconnectedness on the accumulation and retention of beneficial culturally inherited skills (Shennan, 2001; Henrich, 2004; Muthukrishna et al., 2013). A more recent model by Creanza et al. (2017) supported the crucial role of population interaction by ways of migration or exchange, having the same effect as a simple increase in numbers. Grove (2016) also showed that population density had the same effects as higher levels of mobility on cultural transmission, pointing to a crucial role of considering both factors. These approaches share similar ideas with complex systems theory, which found that both the interconnectivity and number of agents play a crucial role in governing cultural complexity and change (Kauffman, 2000; Bentley and Maschner, 2003; Kohler, 2012). Phrased simply, cumulative culture requires both specific cognitive capacities and the right social environment to succeed, the latter also affected by the physical environment, ecosystem, and climate.

These ideas have also been applied to the MSA and the origins of modern humans more recently. Powell et al. (2009) modeled the emergence of so-called modern behavior within a metapopulation model and argued that the emergence and maintenance of complex culture relies on the attainment of critical levels of population density, migratory patterns, and interactions required for stable cultural transmission. In other words, after reaching a demographic tipping point, population density is high enough to successfully maintain culturally transmitted information over long periods in which the rate of accumulation of innovations significantly overtakes its loss. Societies with lower population densities and less interconnectedness will thus eventually lose innovations over long timescales. Group-size reduction may have further exposed human societies to significant risks, including societal collapse and extinction (see also Derex et al., 2013). Since the publication of this model, an increasing number of studies in the MSA have invoked demographic factors as potential drivers for the variable patterns of cultural change they observed (e.g., Wadley, 2015; Sealy, 2016; Tryon and Faith, 2016; Scerri et al., 2017; Thompson et al., 2018; Archer, 2021). In one of the most explicit examples, Mackay et al. (2014) attribute patterns of intraregional similarities and differences through time in the southern African MSA lithic record between MIS 5–2 to variable population interaction and cultural transmission.

We can now relate these theoretical observations and specific models to the complex mosaic patterning of innovations observed for the MSA. When combined, they suggest that while the basic cognitive capacities for complex behaviors (e.g., Haidle et al., 2015, 2016) were likely in place by the beginning of the MSA (e.g., Lahr and Foley, 1998; Shea, 2011; Brooks et al., 2018), a change in demographic variables could explain some of the variable and asynchronous innovation, retention and loss of different traits (Table 1) across different African regions as manifested in the archaeological record. The frequent and manifold innovations in various socio-technological domains demonstrate the underlying creativity and cognitive capacities of modern humans throughout the MSA (see also Wadley, 2021). Yet, times of low population densities and a marked population structure with reduced levels of intergroup interaction may have led to the repeated loss of innovations either due to failed transmission or the local extinction of groups (see also Mackay et al., 2014). In such an interpretation, critical thresholds of effective cultural population density, attained through sheer numbers or connections between groups (Powell et al., 2009; Kolodny et al., 2015), appear to have only been reached over long periods after the end of the MSA allowing for the more consistent and exponential patterns of cultural change seen in the LSA, Upper Paleolithic, and Holocene more broadly. On the level of the entire continent, these demographic hypotheses remain speculative and are backed up by relevant archaeological data and rigorous quantitative study only in some parts of Africa (e.g., Powell et al., 2009; Archer, 2021). Analytical testing of such explanatory scenarios on larger spatiotemporal scales will require further modeling that includes multiple demographic and non-demographic factors in a direct engagement with empirical record of the MSA and requires novel approaches to even better reconstruct information networks and population sizes during the Pleistocene (see e.g., French, 2016; Strassberg and Creanza, 2021; Schmid et al., 2022). The appearance of innovations in the MSA record alongside evidence of increased task specialization is unlikely to be independent. Research in sociology and economics has long suggested that societies with larger populations allow more specialization and division of labor, both of which add to the corpus of information possessed by the group (e.g., Durkheim, 1893; Ofek, 2001).

How do these considerations fit into the broader picture of the biocultural evolution of *H. sapiens*? In general, novel demographic approaches align with a pan-African structured metapopulation that ensured the continuity of universally shared traits such as the ‘basic MSA’ and whose local and only loosely connected demes were the context of the variable emergence and disappearance of innovations at different places and times. Indeed, along with genetic and fossil information, this cultural data has been used to suggest that both modern human biology and behavior originated within a structured metapopulation (Scerri et al., 2018, 2019). What can be reasonably inferred from newer genetic data, complements these inferences. Specifically, divergences among early *H. sapiens* populations in Africa appear to have been gradual, with longstanding gene flow over tens or even hundreds of thousands of years (Bergström et al., 2020; Wang et al., 2020), rather than clean, treelike, splits. The gradual nature of this mixing is consistent with low migration and an overall low metapopulation size, dampening innovation and its spread, while ensuring that the elements common to all demes persisted.

Such a demographic model may also explain better than a purely cognitive one, why Middle Paleolithic Neanderthals lagged a little behind *H. sapiens* populations in the number, diversity, and frequency of cultural innovations, showing the flaws of interpreting trait lists at face value. Archaeological and genetic evidence suggests a smaller overall metapopulation size and higher inbreeding for Neanderthals compared to early modern humans (Dalén et al., 2012; Bocquet-Appel and Degioanni, 2013; Churchill, 2014; Prüfer et al., 2014; Sikora et al., 2017), with a collapse in structure following Ice Age conditions that was likely a contributing factor to their disappearance in unmixed form (Rodriguez et al., 2018; Vaesen et al., 2019). Complex behaviors and material culture in the MSA as well as the Middle Paleolithic needed a critical density of population to sustain growth and cumulative development. In sum, the spatial heterogeneity seen in the MSA of Africa might not be at all contingent on different levels of cognitive capacities but could be explained in large part by changes in socio-demographic structure, connectivity between groups, and processes of cultural transmission.

If demography underlies patterns of cultural evolution found here, what explains increases in population size, density, and connectedness? While beyond the scope of this paper, demographic changes could result from various ecological or social factors that jump-started a positive feedback loop. Increasing the niche breadth of MSA people (Kandel et al., 2016; d'Errico et al., 2017; Roberts and Stewart, 2018) might have allowed them to expand to new habitats. In connection with more varied habitats, more diverse diets (Clark and Kandel, 2013; Will et al., 2019b; Wadley et al., 2020a) may have buffered against food shortages, decreasing mortality and extinction rates that boosted population sizes. New ways of social organization that increased the interconnectivity between groups can already be seen at the beginning of the MSA in long-distance transport of raw materials (Brooks et al., 2018) but likely increased toward the end of the MSA, such as long-term exchange and/or migration networks suggested by OES beads reaching back to the Late Pleistocene (Stewart et al., 2020; Miller and Wang, 2022).

At the end, we are left with a glaringly obvious lack of a 'revolution' in the archaeological record, which upholds McBrearty and Brooks' (2000) primary thesis that modern human behavior has deep African roots. However, more recent data have also emphasized that viewing this behavior in terms of a gradually emerging, stable package is no longer tenable. Indeed the 'package' concept predates McBrearty and Brooks (2000) and can be linked to the conceptualization of the European Upper Paleolithic (e.g., Mellars, 1989, 1994; Mellars and Stringer 1989). Instead, new work suggests that demographic variables such as low population numbers played a critical role in driving the variable expressions of the modern mind—innovations, their loss, and reinvention. Ultimately, many 'human revolutions' can only be found at the point when human population sizes were able to grow enough to reach a critical mass capable of transcending losses at the local level and permitting culture to become truly cumulative. Even losses and the collapses of civilizations in recent history have shown how easily it is for humanity to take 'backward steps' without this having any implications for cognitive capacity.

5.3. Future perspectives

Much progress has been made in developing theoretical perspectives on human cultural evolution, with recent scholarship steering away from concepts of packages or modernity, in favor of focusing on notions of variability, flexibility, and plasticity (Malafouris, 2010; Shea, 2011; Conard, 2015; Kandel et al., 2016; Roberts and Stewart, 2018), but also engaging with a broader range of potential causal mechanisms. That being said, many models still pursue monocausal explanations, with an exclusive focus on either biology, environment, cognition, or demography. There might, however, be more than one causal factor, and mechanisms are not always hierarchic and independent, particularly in complex systems like human behavior and culture. Triggers and drivers can also (inter-)act in fundamentally different ways on different spatio-temporal scales (Conard, 2001; Bentley and Maschner, 2003; d'Errico and Banks, 2013), or even apply successively (Chamberlin, 1890) as well as in an asynchronous manner in different areas of Africa (e.g., for environmental change see Chase, 2010; Blome et al., 2012; Lahr and Foley, 2016). On top of this, the principles of path dependence and contingency so prevalent in human (evolutionary) history predict that even small initial changes within populations might have resulted in qualitatively different and unexpected outcomes owing to the complexities and connectedness of human societies (Kauffman, 2000; Bentley and Maschner, 2003; Kohler, 2012).

In a recent study modeling cultural evolution, Kolodny et al. (2015) expanded their initial models by looking at both demographic and environmental parameters. As a result, they were able to create more realistic patterns of cultural evolution echoing archaeological patterns, which included exponential and punctuated change but also more complex trajectories for the gain and loss of cultural traits. These findings suggest that cultural change on large scales may be driven by a complex interaction of population size, environmental change, stochastic cultural losses, and population subdivision, but also depending on general cognitive abilities that determine the rates of tool invention. To these factors, human modification of the environment in the form of niche construction can be added both from a modeling perspective (Fogarty and Creanza, 2017) but also borne out by evidence already stretching back to the MSA (Hussain and Will, 2021; Thompson et al., 2021) and accelerating thereafter (Boivin et al., 2016). Models of cultural evolution should also consider constraints and potentials set by human diet, anatomy, biology, and social structure (e.g., Wells and Stock, 2007; Parkington, 2010; Hill et al., 2011; Neubauer et al., 2018; Bruner, 2021), such as a feedback of changes in genetic makeup and neuroanatomy with cognition, society, and culture (e.g., Laland et al., 2010; Hublin et al., 2015; Wynn et al., 2016; Wadley, 2021). Importantly, however, our observations suggest that not all conceivable causal mechanisms will have equal relevance for understanding cultural changes in the MSA. Evidence for the increasing detachment and autonomy of humans from the environment and direct selective pressures hint toward factors such as demography, social structure, and technology-driven feedback with increasing reliance on material culture as becoming ever more important factors in the ongoing cultural evolution of our species. It is perhaps in the intensification of these processes, and their amplifying feedback loops with demography, that the nature and prevalence of complex behaviors in *H. sapiens* can best be seen, in contrast to what is observed in the Neanderthal record.

As shown here, new theoretical lenses of demography, cultural transmission, and multidimensional fitness landscapes can provide helpful bridges between the complex empirical record and further-reaching interpretations. Such approaches require a geographically informed perspective and the acknowledgment of a high likelihood of different demographic and behavioral trajectories within the vast African continent. Novel models for the behavioral evolution of modern humans should thus be spatially explicit, and take environmental, biological, demographic, cultural, material, and social factors into account. These factors interact to form a complex network of causal agents on several scales. Such an approach is consistent with central tenets of emerging theories for the biocultural evolution of our genus more broadly that emphasize the role of multiple interacting pathways of intergenerational information transfer driving evolutionary pathways (e.g., Cavalli-Sforza and Feldman, 1981; Richerson and Boyd, 2005; Laland et al., 2010; Mesoudi, 2011; Jablonka and Lamb, 2014). Providing a holistic view on the mechanisms and trajectory of the cultural evolution of *H. sapiens* in Africa in the 21st century will require both detailed quantitative observation and modeling of interdisciplinary, pan-African empirical data as well as nuanced and carefully adjusted theoretical scenarios. If the past is any guide to the future, the next 20 years of research will provide further unexpected discoveries and novel approaches that will help to improve our current models for the origins of *H. sapiens* behavioral complexity, fleshing out the picture of becoming human. We see our contribution and its relation to the lasting legacy of McBrearty and Brooks (2000) in this spirit.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgments

We are grateful to the Editors-in-Chief for inviting us to contribute to the special issue 'The 50th Anniversary of Journal of Human Evolution: Current and Future Directions in Reconstructing Our Past.' We thank Andrew Kandel and the ROCEEH team for providing the raw data for the location of Middle Stone Age sites in Figure 1. E.M.L.S. and M.W. thank the anonymous reviewers, Alex Mackay, Christian Tryon, and Huw Groucutt for constructive comments and feedback on the content of the manuscript. M.W. thanks Nicholas Conard for encouraging him to work on the Middle Stone Age and the many discussions on all aspects of the behavioral evolution of modern humans. E.M.L.S. acknowledges financial support from the Max Planck Society. M.W. acknowledges financial support by the Deutsche Forschungsgemeinschaft (grants WI 4978/1-1 and WI 4978/3-1). All opinions and mistakes remain our own.

References

Ambrose, S.H., 1998. Chronology of the Later Stone Age and food production in East Africa. J. Archaeol. Sci. 25, 377–392.

Archer, W., 2021. Carrying capacity, population density and the later Pleistocene expression of backed artefact manufacturing traditions in Africa. Philos. Trans. R. Soc. B 376, 20190716.

Archer, W., Pop, C.M., Gunz, P., McPherron, S.P., 2016. What is Still Bay? Human biogeography and bifacial point variability. J. Hum. Evol. 97, 58–72.

Assefa, Z., Asrat, A., Hovers, E., Lam, Y., Pearson, O., Pleurdeau, D., 2018. Engraved ostrich eggshell from the Middle Stone Age contexts of Goda Buticha, Ethiopia. J. Archaeol. Sci. Rep. 17, 723–729.

Backwell, L., d'Errico, F., Wadley, L., 2008. Middle Stone Age bone tools from the Howiesons Poort layers, Sibudu Cave, South Africa. J. Archaeol. Sci. 35, 1566–1580.

Bader, G.D., Forrester, B., Ehlers, L., Velliky, E., MacDonald, B.L., Linstädter, J., 2021. The Forgotten Kingdom. J. Global Arch. 202, 1–12.

Bader, G.D., Sommer, C., Conard, N.J., Wadley, L., 2022. The final MSA of eastern South Africa: A comparative study between Umbeli Belli and Sibhudu. Azania 57, 197–238.

Bar-Yosef, O., 2002. The Upper Paleolithic revolution. Annu. Rev. Anthropol. 31, 363–393.

Barham, L.S. (Ed.), 2000. The Middle Stone Age of Zambia. Western Academic and Specialist Press, Bristol.

Barham, L.S., 2001. Central Africa and the emergence of regional identity in the Middle Pleistocene. In: Barham, L.S., Robson-Brown, P. (Eds.), Human Roots: Africa and Asia in the Middle Pleistocene. Western Academic and Specialist Press, Bristol, pp. 65–80.

Barham, L.S., 2002. Systematic pigment use in the Middle Pleistocene of South Central Africa. Curr. Anthropol. 43, 181–190.

Barham, L.S., 2013. From Hand to Handle: The First Industrial Revolution. Oxford University Press, Oxford.

Barton, N., d'Errico, F., 2012. North African origins of symbolically mediated behaviour and the Aterian. Dev. Quat. Sci. 16, 23–34.

Basell, L.E., 2008. Middle Stone Age (MSA) site distributions in eastern Africa and their relationship to Quaternary environmental change, refugia and the evolution of *Homo sapiens*. Quat. Sci. Rev. 27, 2484–2498.

Bentley, R.A., Maschner, H.D. (Eds.), 2003. Complex Systems and Archaeology: Empirical and Theoretical Applications. University of Utah Press, Salt Lake City.

Berger, L.R., Hawks, J., Dirks, P.H., Elliott, M., Roberts, E.M., 2017. *Homo naledi* and Pleistocene hominin evolution in subequatorial Africa. eLife 6, e24234.

Bergström, A., McCarthy, S.A., Hui, R., Almarri, M.A., Ayub, Q., Danecek, P., Chen, Y., Felkel, S., Hallast, P., Kamm, J., Blanché, H., Deleuze, J.-F., Cann, H., Mallick, S., Reich, D., Sandhu, M.S., Skoglund, P., Scally, A., Xue, Y., Durbin, R., Tyler-Smith, C., 2020. Insights into human genetic variation and population history from 929 diverse genomes. Science 367, 6484.

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

Binford, L.R., 1981. Bones. Ancient Myths and Modern Men. Academic Press, Boston, p. 320.

Binford, L.R., 1989. Styles of style. J. Anthropol. Archaeol. 8, 51–67.

Blessing, M.A., Conard, N.J., Will, M., in press. Lithic standardization and behavioral complexity in the Middle Stone Age. A case study from Sibhudu, South Africa. Lithic Technol. 1–15. https://doi.org/10.1080/01977261.2022.2158591.

Blinkhorn, J., Grove, M., 2018. The structure of the Middle Stone Age of eastern Africa. Quat. Sci. Rev. 195, 1–20.

Blinkhorn, J., Grove, M., Timbrell, L., Scerri, E.M.L., 2022. Evaluating refugia in recent human evolution in Africa. Philos. Trans. R. Soc. B 377, 20200485.

Blegen, N., Jicha, B.R., McBrearty, S., 2018. A new tephrochronology for early diverse stone tool technologies and long-distance raw material transport in the Middle to Late Pleistocene Kapthurin Formation, East Africa. J. Hum. Evol. 121, 75–103.

Blome, M.W., Cohen, A.S., Tryon, C.A., Brooks, A.S., Russell, J., 2012. The environmental context for the origins of modern human diversity: A synthesis of regional variability in African climate 150,000-30,000 years ago. J. Hum. Evol. 62, 563–592.

Bocquet-Appel, J., Degioanni, A., 2013. Neanderthal demographic estimates. Curr. Anthropol. 54, 202–2013.

Boivin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M., Denham, T., Petraglia, M.D., 2016. Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. Proc. Natl. Acad. Sci. USA 113, 6388–6396.

Botha, R., 2010. On the soundness of inferring modern language from symbolic behaviour. Camb. Archaeol. J. 20, 345–356.

Bouzouggar, A., Barton, R.N.E., Vanhaeren, M., d'Errico, F., Collcutt, S., Higham, T., Hodge, E., Parfitt, S., Rhodes, E., Schwnninger, J.-L., Stringer, C., Turner, E., Ward, S., Moutmir, A., Stambouli, A., 2007. 82,000-year old shell beads from North Africa and implications for the origins of modern human behavior. Proc. Natl. Acad. Sci. USA 104, 9964–9969.

Braucher, R., Oslisly, R., Mesfin, I., Ntoutoume, P., ASTER Team, 2022. In situ-produced 10Be and 26Al indirect dating of Elarmékora Earlier Stone Age artefacts: First attempt in a savannah forest mosaic in the middle Ogooué valley, Gabon. Philos. Trans. R. Soc. B 377, 20200482.

Braun, D.R., Faith, J.T., Douglass, M.J., Davies, B., Power, M.J., Aldeias, V., Conard, N.J., Cutts, R., DeSanstis, L.R.G., Dupont, L.M., Esteban, I., Kandel, A.W., Levin, N.E., Luyt, J., Parkington, J., Pickering, R., Quick, L., Sealy, J., Stynder, D., 2021. Ecosystem engineering in the Quaternary of the West Coast of South Africa. Evol. Anthropol. 30, 50–62.

Bräuer, G., 1984. A craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans. In: Smith, F.H., Spencer, F. (Eds.), The Origins of Modern Humans: A World Survey of the Fossil Evidence. Liss, New York, pp. 327–410.

Bräuer, G., 1989. The ES-11693 hominid from West Turkana and *Homo sapiens* evolution in East Africa. Hominidae 1989, 241–245.

Brooks, A.S., Yellen, J.E., Potts, R., Behrensmeyer, A.K., Deino, A.L., Leslie, D.E., Ambrose, S.H., Ferguson, J.R., d'Errico, F., Zipkin, A.M., Whittaker, S., Post, J., Veatch, E.G., Foecke, K., Clark, J.B., 2018. Long-distance stone transport and pigment use in the earliest Middle Stone Age. Science 360, 90–94.

Brown, K.S., Marean, C.W., Herries, A.I., Jacobs, Z., Tribolo, C., Braun, D., Roberts, D.L., Meyer, M.C., Bernatchez, J., 2009. Fire as an engineering tool of early modern humans. Science 325, 859–862.

Brown, K.S., Marean, C.W., Jacobs, Z., Schoville, B.J., Oestmo, S., Fisher, E.C., Bernatchez, J., Karkanas, P., Matthews, T., 2012. An early and enduring advanced technology originating 71,000 years ago in South Africa. Nature 491, 590–593.

Bruner, E., 2021. Evolving human brains: Paleoneurology and the fate of Middle Pleistocene. J. Archaeol. Method Theory 28, 76–94.

Campmas, E., 2018. Integrating human-animal relationships into new data on Aterian complexity: A paradigm shift for the North African Middle Stone Age. Afr. Archaeol. Rev. 34, 469–491.

Cann, R.L., Stoneking, M., Wilson, A.C., 1987. Mitochondrial DNA and human evolution. Nature 325, 31–36.

Cavalli-Sforza, L.L., Feldman, M.W., 1981. Cultural Transmission and Evolution: A Quantitative Approach. Princeton University Press, Princeton.

Chamberlin, T.C., 1890. The method of multiple working hypotheses. Science 366, 92–96.

Chazan, M., Berna, F., Brink, J., Ecker, M., Holt, S., Porat, N., Thorpe, J., Horwitz, L.K., 2020. Archeology, environment, and chronology of the Early Middle Stone Age component of Wonderwerk Cave. J. Paleolit. Archaeol. 3, 302–335.

Chase, B.M., 2010. South African palaeoenvironments during marine oxygen isotope stage 4: A context for the Howiesons Poort and Still Bay industries. J. Archaeol. Sci. 37, 1359–1366.

Chevrier, B., Rasse, M., Lespez, L., Tribolo, C., Hajdas, I., Guardiola Figols, M., Lebrun, B., Leplongon, A., Camara, A., Huysecom, E., 2016. West African Palaeolithic history: New archaeological and chronostratigraphic data from the Falémé Valley, Eastern Senegal. Quat. Int. 408, 33–52.

Chevrier, B., Soriano, S., Rasse, M., Lespez, L., Lebrun, B., Tribolo, C., 2018. Between continuity and discontinuity: An overview of the West African Paleolithic over the last 200,000 years. Quat. Int. 466, 3–22.

Churchill, S.E., 2014. Thin on the Ground: Neandertal Biology, Archeology and Ecology. John Wiley and Sons, Hoboken.

Clark, J.D., 1959. The Prehistory of Southern Africa. Penguin Books, London.

Clark, J.D., 1982. The cultures of the Middle Paleolithic and Middle Stone Age. In: Clark, J.D. (Ed.), The Cambridge History of Africa, Vol. 1: From the Earliest Times to 500 BC. Cambridge University Press, Cambridge, pp. 248–342.

Clark, J.D., 1988. The Middle Stone Age of east Africa and the beginnings of regional identity. J. World Prehist. 2, 237–305.

Clark, J.D., 2001. Kalambo Falls Prehistoric Site, Vol. III. The Earlier Cultures: Middle and Earlier Stone Age. Cambridge University Press, Cambridge.

Clark, J.D., Kleindienst, M.R., 2001. The Stone Age cultural sequence: Terminology, typology and raw material. In: Clark, J.D. (Ed.), Kalambo Falls Prehistoric Site, Vol. III. The Earlier Cultures: Middle and Earlier Stone Age. Cambridge University Press, Cambridge, pp. 34–65.

Clark, J.D., Cole, G.H., Isaac, G.L., Kleindienst, M.R., 1966. Precision and definition in African archaeology. S. Afr. Archaeol. Bull. 21, 114–121.

Clark, J.D., Schultz, D.U., Kroll, E.M., Freedman, E.E., Galloway, A., Batkin, J., Kurashina, H., 2008. The Aterian of Adrar Bous and the Central Sahara. In: Gifford-Gonzalez, D. (Ed.), Adrar Bous, Archaeology of a Central Saharan Granitic Ring Complex in Niger. Royal Museum for Central Africa, Tervuren, pp. 91–163.

Clark, J.L., 2013. Exploring the relationship between climate change and the decline of the Howieson's Poort at Sibudu Cave (South Africa). In: Clark, J.L., Speth, J. (Eds.), Zooarchaeology and Modern Human Origins: Human Hunting Behavior during the Later Pleistocene. Springer Science, Dordrecht, pp. 9–18.

Clark, J.L., Kandel, A.W., 2013. The evolutionary implications of variation in human hunting strategies and diet breadth during the Middle Stone Age of southern Africa. Curr. Anthropol. 54, 269–287.

Coolidge, F.L., Haidle, M.N., Lombard, M., Wynn, T., 2016. Bridging theory and bow hunting: Human cognitive evolution and archaeology. Antiquity 90, 219–228.

Conard, N.J., 2001. The future of archaeology. In: Kobylinski, Z. (Ed.), Quo Vadis Archaeologia? Whither European Archaeology in the 21st Century? Polish Academy of Sciences, Warsaw, pp. 106–117.
Conard, N.J., 2005. An overview of the patterns of behavioral change in Africa and Eurasia during the Middle and Late Pleistocene. In: d'Errico, F., Blackwell, L. (Eds.), From Tools to Symbols: From Early Hominids to Modern Humans. Witwatersrand University Press, Johannesburg, pp. 294–332.
Conard, N.J., 2008. A critical view of the evidence for a southern African origin of behavioural modernity. S. Afr. Archaeol. Bull. 10, 175–179.
Conard, N.J., 2015. Cultural evolution during the Middle and Late Pleistocene in Africa and Eurasia. In: Henke, W., Tattersall, I. (Eds.), Handbook of Paleoanthropology. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 2465–2508.
Conard, N.J., Will, M., 2015. Examining the causes and consequences of short-term behavioral change during the Middle Stone Age at Sibudu, South Africa. PLoS One 10, e0130001.
Conard, N.J., Porraz, G., Wadley, L., 2012. What is in a name? Characterizing the Post-Howiesons Poort at Sibudu. S. Afr. Archaeol. Bull. 67, 180–199.
Creanza, N., Kolodny, O., Feldman, M.W., 2017. Greater than the sum of its parts? Modelling population contact and interaction of cultural repertoires. J. R. Soc. Interface 14, 20170171.
Dalén, L., Orlando, L., Shapiro, B., Brandström-Durling, M., Quam, R., Thomas, M., Gilbert, P., Diez Fernández-Lomana, J.C., Willerslev, E., Arsuaga, J.L., Götherström, A., 2012. Partial genetic turnover in Neandertals: Continuity in the East and population replacement in the West. Mol. Biol. Evol. 29, 1893–1897.
Dapschauskas, R., Göden, M.B., Sommer, C., Kandel, A.W., 2022. The emergence of habitual ochre use in Africa and its significance for the development of ritual behavior during the Middle Stone Age. J. World Prehist. 35, 233–319.
Dayet, L., Texier, P.J., Daniel, F., Porraz, G., 2013. Ochre resources from the Middle Stone Age sequence of Diepkloof Rock Shelter, Western Cape, South Africa. J. Archaeol. Sci. 40, 3492–3505.
Deacon, H.J., Wurz, S., 2001. Middle Pleistocene populations and the emergence of modern behaviour. In: Barham, L.S., Robson-Brown, K. (Eds.), Human Roots: Africa and Asia in the Middle Pleistocene. Western Academic and Specialist Press, Bristol, pp. 55–63.
Deino, A.L., Behrensmeyer, A.K., Brooks, A.S., Yellen, J.E., Sharp, W.D., Potts, R., 2018. Chronology of the Acheulean to Middle Stone Age transition in eastern Africa. Science 360, 95–98.
Derex, M., Beugin, M.-P., Godelle, B., Raymond, M., 2013. Experimental evidence for the influence of group size on cultural complexity. Nature 503, 389–391.
Dibble, H.L., Aldeias, V., Alvarez-Fernández, E., Blackwell, B.A.B., Hallet-Desguez, E., Jacobs, Z., Goldberg, P., Lin, S.C., Morala, A., Meyer, M.C., Olszewski, D.I., Reed, K.E., Reed, D.N., Režek, Ž., Richter, D., Roberts, R.G., Sandgathe, D.M., Schurmans, U.A., Skinner, A.R., Steele, T.E., El-Hajraoui, M., 2012. New excavations at the site of Contrebandiers cave, Morocco. PaleoAnthropology 2012, 145–201.
Doerschner, N., Fitzsimmons, K.E., Ditchfield, P., McLaren, S.J., Steele, T.E., Zielhofer, C., McPherron, S.P., Bouzouggar, A., Hublin, J.-J., 2016. A new chronology for Rhafas, Northeast Morocco, spanning the North African Middle Stone Age through to the Neolithic. PLoS One 11, e0162280.
Doronicheva, E.V., Golovanova, L.V., Doronichev, V.B., Shackley, M.S., Nedomolkin, A.G., 2019. New data about exploitation of the Zayukovo (Baksan) obsidian source in Northern Caucasus during the Paleolithic. J. Archaeol. Sci. Rep. 23, 157–165.
Douze, K., Delagnes, A., 2016. The pattern of emergence of a Middle Stone Age tradition at Gademotta and Kulkuletti (Ethiopia) through convergent tool and point technologies. J. Hum. Evol. 91, 93–121.
Douze, K., Delagnes, A., Rots, V., Gravina, B., 2018. A reply to Sahle and Braun's reply to 'The pattern of emergence of a Middle Stone Age tradition at Gademotta and Kulkuletti (Ethiopia) through convergent tool and point technologies', [J. Hum. Evol. 91 (2016) 93–121]. J. Hum. Evol. 125, 207–214.
Douze, K., Lespez, L., Rasse, M., Tribolo, C., Garnier, A., Lebrun, B., Mercier, N., Ndiaye, M., Chevrier, B., Huysecom, E., 2021. A West African Middle Stone Age site dated to the beginning of MIS 5: Archaeology, chronology, and paleoenvironment of the Ravin Blanc I (eastern Senegal). J. Hum. Evol. 154, 102952.
Dunbar, R.I.M., 2003. The social brain: Mind, language, and society in evolutionary perspective. Annu. Rev. Anthropol. 32, 163–181.
Durkheim, E., 1893. The Division of Labour in Society. The Free Press, New York.
Dusseldorp, G.L., 2010. Prey choice during the South African Middle Stone Age: Avoiding dangerous prey or maximising returns? Afr. Archaeol. Rev. 27, 107–133.
d'Errico, F., 2003. The invisible frontier. A multiple species model for the origin of behavioral modernity. Evol. Anthropol. 12, 188–202.
d'Errico, F., Stringer, C.B., 2011. Evolution, revolution or saltation scenario for the emergence of modern cultures? Philos. Trans. R. Soc. B 366, 1060–1069.
d'Errico, F., Banks, W., 2013. Identifying mechanisms behind Middle Paleolithic and Middle Stone Age cultural trajectories. Curr. Anthropol. 54, 371–387.
d'Errico, F., Backwell, L., 2016. Earliest evidence of personal ornaments associated with burial: The Conus shells from Border Cave. J. Hum. Evol. 93, 91–108.
d'Errico, F., Henshilwood, C.S., Vanhaeren, M., van Niekerk, K., 2005. Nassarius kraussianus shell beads from Blombos Cave: Evidence for symbolic behaviour in the Middle Stone Age. J. Hum. Evol. 48, 2–14.
d'Errico, F., Vanhaeren, M., Barton, N., Bouzouggar, A., Mienis, H., Richter, D., Hublin, J.-J., McPherron, S.P., Lozouet, P., 2009. Additional evidence on the use of personal ornaments in the Middle Paleolithic of North Africa. Proc. Natl. Acad. Sci. USA 106, 16051–16056.
d'Errico, F., Backwell, L.R., Wadley, L., 2012. Identifying regional variability in Middle Stone Age bone technology: The case of Sibudu Cave. J. Archaeol. Sci. 39, 2479–2495.
d'Errico, F., Banks, W.E., Warren, D.L., Sgubin, G., van Niekerk, K., Henshilwood, C., Daniau, A.-L., Sánchez Goñi, M.F., 2017. Identifying early modern human ecological niche expansions and associated cultural dynamics in the South African Middle Stone Age. Proc. Natl. Acad. Sci. USA 114, 7869–7876.
Faith, J.T., 2008. Eland, buffalo, and wild pigs: Were Middle Stone Age humans ineffective hunters? J. Hum. Evol. 55, 24–36.
Fogarty, L., Creanza, N., 2017. The niche construction of cultural complexity: Interactions between innovations, population size and the environment. Philos. Trans. R. Soc. B 372. https://doi.org/10.1098/rstb.2016.0428.
Foley, R.A., Lahr, M.M., 2015. Lithic landscapes: Early human impact from stone tool production on the central Saharan environment. PLoS One 10, e0116482.
French, J.C., 2016. Demography and the Palaeolithic archaeological record. J. Archaeol. Method Theory 23, 150–199.
Gabucio, M.J., Fernández-Laso, M.C., Rosell, J., 2018. Turning a rock shelter into a home. Neanderthal use of space in Abric Romaní levels M and O. Hist. Biol. 30, 743–766.
Gamble, C., 1982. Interaction and alliance in Palaeolithic Society. MAN New Series 17, 92–107.
Gamble, C., 2007. Origins and Revolutions: Human Identity in Earliest Prehistory. Cambridge University Press, Cambridge.
Gilbert, W., Doronichev, V., Golovanova, L., Morgan, L., Nunez, L., Renne, P., 2016. Archaeology and context of Hugub, an important new Late Acheulean locality in Ethiopia's Northern Rift. PaleoAnthropology 2016, 58–99.
Goldberg, P., Miller, C.E., Schiegl, S., Ligouis, B., Berna, F., Conard, N.J., Wadley, L., 2009. Bedding, hearths, and site maintenance in the Middle Stone age of Sibudu cave, KwaZulu-Natal, South Africa. Archaeol. Anthropol. Sci. 1, 95–122.
Goodwin, A.J.H., 1928. An introduction to the Middle Stone Age in South Africa. S. Afr. J. Sci. 25, 410–418.
Goodwin, A.J.H., van Riet Lowe, C., 1929. The Stone Age cultures of South Africa. Ann. S. Afr. Mus. 27, 1–289.
Grine, F.E., Klein, R.G., Volman, T.P., 1991. Dating, archaeology and human fossils from the Middle Stone Age levels of Die Kelders, South Africa. J. Hum. Evol. 21, 363–395.
Groucutt, H.S., 2014. Middle Palaeolithic point technology, with a focus on the site of Tor Faraj (Jordan, MIS 3). Quat. Int. 350, 205–226.
Groucutt, H.S., Scerri, E.M., Stringer, C., Petraglia, M.D., 2019. Skhul lithic technology and the dispersal of *Homo sapiens* into Southwest Asia. Quat. Int. 515, 30–52.
Grove, M., 2016. Population density, mobility, and cultural transmission. J. Archaeol. Sci. 74, 75–84.
Grün, R., Beaumont, P.B., 2001. Border Cave revisited: A revised ESR chronology. J. Hum. Evol. 40, 467–482.
Gunz, P., Bookstein, F.L., Mitteroecker, P., Stadlmayr, A., Seidler, H., Weber, G.W., 2009. Early modern human diversity suggests subdivided population structure and a complex out-of-Africa scenario. Proc. Natl. Acad. Sci. USA 106, 6094–6098.
Haidle, M.N., 2010. Working-memory capacity and the evolution of modern cognitive potential: Implications from animal and early human tool use. Curr. Anthropol. 51, 149–166.
Haidle, M.N., 2014. Building a bridge—an archaeologist's perspective on the evolution of causal cognition. Front. Psychol. 5, 1–15.
Haidle, M.N., 2016. Lessons from Tasmania–cultural performance versus cultural capacity. In: Haidle, M.N., Conard, N.J., Bolus, M. (Eds.), The Nature of Culture. Springer, Dordrecht, pp. 7–17.
Haidle, M.N., Bolus, M., Collard, M., Conard, N.J., Garofoli, D., Lombard, M., Nowell, A., Tennie, C., Whiten, A., 2015. The nature of culture: An eight-grade model for the evolution and expansion of cultural capacities in hominins and other animals. J. Anthropol. Sci. 93, 1–28.
Haidle, M.N., Conard, N.J., Bolus, M., 2016. The nature of culture: Research goals and new directions. In: Haidle, M.N., Conard, N.J., Bolus, M. (Eds.), The Nature of Culture. Springer, Dordrecht, pp. 1–6.
Hallett, E.Y., Marean, C.W., Steele, T.E., Álvarez-Fernández, E., Jacobs, Cerasoni, J.N., Aldeias, V., Scerri, E.M.L., Olszewski, D.I., El Hajraoui, M.A., Dibble, H.L., 2021. A worked bone assemblage from 120,000–90,000 year old deposits at Contrebandiers Cave, Atlantic Coast, Morocco. iScience 24, 102988.
Harari, Y.N., 2014. Sapiens: A Brief History of Humankind. Penguin Random House, Gütersloh.
Harvati, K., Stringer, C., Grün, R., Aubert, M., Allsworth-Jones, P., Folorunso, C.A., 2011. The Later Stone Age calvaria from Iwo Eleru, Nigeria: Morphology and chronology. PLoS One 6, e24024.
Henrich, J., 2001. Cultural transmission and the diffusion of innovations: Adoption dynamics indicate that biased cultural transmission is the predominate force in behavioural change. Am. Anthropol. 103, 992–1013.
Henrich, J., 2004. Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses: The Tasmanian case. Am. Antiq. 69, 197–214.
Henry, A.G., Brooks, A.S., Piperno, D.R., 2014. Plant foods and the dietary ecology of Neanderthals and early modern humans. J. Hum. Evol. 69, 44–54.
Henshilwood, C.S., Marean, C.W., 2003. The origin of modern human behavior. Critique of the models and their test implications. Curr. Anthropol. 44, 627–651.

Henshilwood, C.S., Marean, C.W., 2006. Remodelling the origins of modern human behaviour. In: Soodyall, H. (Ed.), The Human Genome and Africa: Tracing the Lineage of Modern Man. Jonathan Ball, Cape Town, pp. 31–46.
Henshilwood, C.S., d'Errico, F., Marean, C.W., Milo, R.G., Yates, R., 2001. An early bone tool industry from the Middle Stone Age at Blombos Cave, South Africa: Implications for the origins of modern human behaviour, symbolism and language. J. Hum. Evol. 41, 631–678.
Henshilwood, C.S., d'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G.A.T., Mercier, N., Sealy, J.C., Valladas, H., Watts, I., Wintle, A.G., 2002. Emergence of modern human behavior: Middle Stone Age engravings from South Africa. Science 295, 1278–1280.
Henshilwood, C., d'Errico, F., Vanhaeren, M., van Niekerk, K., Jacobs, Z., 2004. Middle Stone Age shell beads from South Africa. Science 304, 404.
Henshilwood, C.S., d'Errico, F., Watts, I., 2009. Engraved ochres from the Middle Stone Age levels at Blombos Cave, South Africa. J. Hum. Evol. 57, 27–47.
Henshilwood, C.S., d'Errico, F., van Niekerk, K.L., Coquinot, Y., Jacobs, Z., Lauritzen, S.-E., 2011. A 100,000-year-old ochre-processing workshop at Blombos Cave, South Africa. Science 334, 219–222.
Henshilwood, C.S., Van Niekerk, K.L., Wurz, S., Delagnes, A., Armitage, S.J., Rifkin, R.F., Douze, K., Keene, P., Haaland, M.M., Reynard, J., Discamps, E., Mienies, S.S., 2014. Klipdrift Shelter, Southern Cape, South Africa: Preliminary report on the Howiesons Poort layers. J. Archaeol. Sci. 45, 284–303.
Henshilwood, C.S., d'Errico, F., Van Niekerk, K.L., Dayet, L., Queffelec, A., Pollarolo, L., 2018. An abstract drawing from the 73,000-year-old levels at Blombos Cave, South Africa. Nature 562, 115–118.
Herries, A.I., 2011. A chronological perspective on the Acheulian and its transition to the Middle Stone Age in southern Africa: The question of the Fauresmith. Int. J. Ecol. Biol. 2011, 961401.
Hill, K.R., Walker, R.S., Božičević, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A.M., Marlowe, F., Wiessner, P., Wood, B., 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. Science 33, 1286–1289.
Hodgskiss, T., 2012. Attribute analysis of the Sibudu Middle Stone Age ochre assemblage. South. Afr. Humanit. 24, 99–120.
Högberg, A., Lombard, M., 2020. 'I can do it' becomes 'we do it': Kimberley (Australia) and Still Bay (South Africa) points through a socio-technical framework lens. J. Paleolit. Archaeol. 3, 633–663.
Hublin, J.-J., 1992. Recent human evolution in northwestern Africa. Philos. Trans. R. Soc. B 337, 185–191.
Hublin, J.-J., Neubauer, S., Gunz, P., 2015. Brain ontogeny and life history in Pleistocene hominins. Philos. Trans. R. Soc. B 370, 20140062.
Hublin, J.-J., Ben-Ncer, A., Bailey, S.E., Freidline, S.E., Neubauer, S., Skinner, M.M., Bergmann, I., Le Cabec, A., Benazzi, S., Harvati, K., Gunz, P., 2017. New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. Nature 546, 289.
Hussain, S.T., Will, M., 2021. Materiality, agency and evolution of lithic technology: An integrated perspective for Palaeolithic archaeology. J. Archaeol. Method Theory 28, 617–670.
Jablonka, E., Lamb, M.J., 2014. Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life, Revised Edition. MIT Press, Cambridge.
Jacobs, Z., Roberts, R.G., Galbraith, R.F., Deacon, H.J., Grün, R., Mackay, A., Mitchell, P., Vogelsang, R., Wadley, L., 2008. Ages for the Middle Stone Age of southern Africa: Implications for human behaviour and dispersal. Science 322, 733–735.
Kandel, A.W., Bolus, M., Bretzke, K., Bruch, A.A., Haidle, M.N., Hertler, C., Märker, M., 2016. Increasing behavioral flexibility? An integrative macro-scale approach to understanding the Middle Stone Age of southern Africa. J. Archaeol. Method Theory 23, 623–668.
Kauffman, S.A., 2000. Investigations. Oxford University Press, Oxford.
Key, A.J., Jarić, I., Roberts, D.L., 2021. Modelling the end of the Acheulean at global and continental levels suggests widespread persistence into the Middle Palaeolithic. Humanit. Soc. Sci. Commun. 8, 1–12.
Klein, R.G., 1970. Problems in the study of the Middle Stone Age of South Africa. S. Afr. Archaeol. Bull. 25, 127–135.
Klein, R.G., 1994. The problem of modern human origins. In: Nitecki, M.H., Nitecki, D.V. (Eds.), Origins of Anatomically Modern Humans. Plenum Press, New York, pp. 3–17.
Klein, R.G., 2000. Archeology and the evolution of human behavior. Evol. Anthropol. 9, 17–36.
Klein, R.G., 2008. Out of Africa and the evolution of human behaviour. Evol. Anthropol. 17, 267–281.
Klein, R.G., 2009. The Human Career: Human Biological and Cultural Origins, 3rd ed. University of Chicago Press, Chicago.
Klein, R.G., Edgar, B., 2002. The Dawn of Human Culture. John Wiley and Sons, New York.
Klein, R.G., Avery, G., Cruz-Uribe, K., Halkett, D., Hart, T., Milo, R.G., Volman, T.P., 1999. Duinefontein 2: An Acheulean site in the Western Cape province of South Africa. J. Hum. Evol. 37, 153–190.
Kohler, T.A., 2012. Complex systems and archaeology. In: Hodder, I. (Ed.), Archaeological Theory Today, 2nd ed. Polity Press, Cambridge, pp. 93–123.
Kolodny, O., Creanza, N., Feldman, M., 2015. Evolution in leaps: The punctuated accumulation and loss of cultural innovations. Proc. Natl. Acad. Sci. USA 112, E6762–E6769.
Kuhn, S.L., 2006. Trajectories of change in the Middle Paleolithic in Italy. In: Hovers, E., Kuhn, S.L. (Eds.), Transitions before the Transition: Evolution and Stability in the Middle Paleolithic and Middle Stone Age. Springer, New York, pp. 109–120.
Kuman, K., 2014. Acheulean industrial complex. In: Smith, C. (Ed.), Encyclopedia of Global Archaeology. Springer, New York.
Kuman, K., Lotter, M.G., Leader, G.M., 2020. The Fauresmith of South Africa: A new assemblage from Canteen Kopje and significance of the technology in human and cultural evolution. J. Hum. Evol. 148, 102884.
Kyriacou, K., Parkington, J.E., Marais, A.D., Braun, D.R., 2014. Nutrition, modernity and the archaeological record: Coastal resources and nutrition among Middle Stone Age hunter-gatherers on the western Cape coast of South Africa. J. Hum. Evol. 77, 64–73.
Lahr, M.M., 2016. The shaping of human diversity: Filters, boundaries and transitions. Philos. Trans. R. Soc. B 371, 20150241.
Lahr, M.M., Foley, R.A., 1998. Towards a theory of modern human origins: Geography, demography, and diversity in recent human evolution. Am. J. Phys. Anthropol. 107, 137–176.
Lahr, M.M., Foley, R.A., 2016. Human evolution in late Quaternary eastern Africa. In: Jones, S.C., Stewart, B.A. (Eds.), Africa from MIS 6-2: Population Dynamics and Paleoenvironments. Springer, Dordrecht, pp. 215–231.
Laland, K.N., Odling-Smee, J., Feldman, M.W., 2000. Niche construction, biological evolution, and cultural change. Behav. Brain Sci. 23, 131–146.
Laland, K.N., Odling-Smee, J., Myles, S., 2010. How culture shaped the human genome: Bringing genetics and the human sciences together. Nat. Rev. Genet. 11, 137–148.
Lechtman, H., 1977. Style in technology – some early thoughts. In: Lechtman, H., Merill, R.S. (Eds.), Material Culture. Styles, Organisation, and Dynamics of Technology. 1975 Proceedings of the American Ethnological Society. West Publishing, St Paul, pp. 3–20.
Li, H., Kuman, K., Lotter, M.G., Leader, G.M., Gibbon, R.J., 2017. The Victoria West: Earliest prepared core technology in the Acheulean at Canteen Kopje and implications for the cognitive evolution of early hominids. R. Soc. Open Sci. 4, 170288.
Logan, C.J., Avin, S., Boogert, N., Buskell, A., Cross, F.R., Currie, A., Jelbert, S., Lukas, D., Mares, R., Navarrete, A.F., Shigeno, S., Montgomery, S.H., 2018. Beyond brain size: Uncovering the neural correlates of behavioural and cognitive specialization. Comp. Cogn. Behav. Rev. 13, 55–89.
Lombard, M., 2006. Direct evidence for the use of ochre in the hafting technology of Middle Stone Age tools from Sibudu Cave. South. Afr. Humanit. 18, 57–67.
Lombard, M., 2009. The Howieson's Poort of South Africa amplified. S. Afr. Archaeol. Bull. 64, 4–12.
Lombard, M., 2012. Thinking through the Middle Stone Age of sub-Saharan Africa. Quat. Int. 270, 140–155.
Lombard, M., 2016. Mountaineering or ratcheting? Stone Age hunting weapons as proxy for the evolution of human technological, behavioral and cognitive flexibility. In: Haidle, M.N., Conard, N.J., Bolus, M. (Eds.), The Nature of Culture. Springer, New York, pp. 135–146.
Lombard, M., Phillipson, L., 2010. Indications of bow and stone-tipped arrow use 64 000 years ago in KwaZulu-Natal, South Africa. Antiquity 84, 635–648.
Lombard, M., Haidle, M., 2012. Thinking a bow-and-arrow set: Cognitive implications of Middle Stone Age bow and stone-tipped arrow technology. Camb. Archaeol. J. 22, 237–264.
Lotter, M.G., Kuman, K., 2018. The Acheulean in South Africa, with announcement of a new site (Penhill Farm) in the lower Sundays River Valley, Eastern Cape Province, South Africa. Quat. Int. 480, 43–65.
Mackay, A., Stewart, B.A., Chase, B.M., 2014. Coalescence and fragmentation in the Late Pleistocene archaeology of southernmost Africa. J. Hum. Evol. 72, 26–51.
Mackay, A., Armitage, S.J., Niespolo, E.M., Sharp, W.D., Stahlschmidt, M.C., Blackwood, A.F., Boyd, K.C., Chase, B.M., Lagle, S.E., Kaplan, C.F., Low, M.A., Martisius, N.L., McNeill, P.J., Moffat, I., O'Driscoll, C.A., Rudd, R., Orton, J., Steele, T.E., 2022. Environmental influences on human innovation and behavioural diversity in southern Africa 92–80 thousand years ago. Nat. Ecol. Evol. 6, 361–369.
Martinón-Torres, M., d'Errico, F., Santos, E., Álvaro Gallo, A., Amano, N., Archer, W., Armitage, S.J., Arsuaga, J.L., Bermúdez de Castro, J.M., Blinkhorn, J., Crowther, A., Douka, K., Dubernet, S., Faulkner, P., Fernández-Colón, P., Kourampas, N., González García, J., Larreina, D., Le Bourdonnec, F.-X., MacLeod, G., Martín-Francés, L., Massilani, D., Mercader, J., Miller, J.M., Ndiema, E., Notario, B., Martí, A.P., Prendergast, M.E., Queffelec, A., Rigaud, S., Roberts, P., Shoaee, M.J., Shipton, C., Simpson, I., Petraglia, N.B., Petraglia, M.D., 2021. Earliest known human burial in Africa. Nature 593, 95–100.
Malafouris, L., 2010. Metaplasticity and the human becoming: Principles of neuroarchaeology. J Anthropol. Sci. 88, 49–72.
Mallick, S., Li, H., Lipson, M., Mathieson, I., Gymrek, M., Racimo, F., Zhao, M., Chennagiri, N., Nordenfelt, S., Tandon, A., Skoglund, P., Lazaridis, I., Sankararaman, S., Fu, Q., Rohland, N., Renaud, G., Erlich, Y., Willems, T., Gallo, C., Spence, J.P., Song, Y.S., Poletti, G., Balloux, F., van Driem, G., de Knijff, P., Romero, I.G., Jha, A.R., Behar, D.M., Bravi, C.M., Capelli, C., Hervig, T., Moreno-Estrada, A., Posukh, O.L., Balanovska, E., Balanovsky, O., Karachanak-Yankova, S., Sahakyan, H., Toncheva, D., Yepiskoposyan, L., Tyler-Smith, C., Xue, Y., Abdullah, M.S., Ruiz-Linares, A., Beall, C.M., Di Rienzo, A., Jeong, C., Starikovskaya, E.B., Metspalu, E., Parik, J., Villems, R., Henn, B.M., Hodoglugil, U., Mahley, R., Sajantila, A., Stamatoyannopoulos, G., Wee, J.T., Khusainova, R., Khusnutdinova, E., Litvinov, S., Ayodo, G., Comas, D., Hammer, M.F., Kivisild, T., Klitz, W., Winkler, C.A., Labuda, D., Bamshad, M., Jorde, L.B., Tishkoff, S.A., Watkins, W.S., Metspalu, M., Dryomov, S., Sukernik, R., Singh, L., Thangaraj, K.,

Pääbo, S., Kelso, J., Patterson, N., Reich, D., 2016. The Simons genome diversity project: 300 genomes from 142 diverse populations. Nature 538, 201–206.
Marean, C.W., 2010. Pinnacle Point Cave 13B (Western Cape Province, South Africa) in context: The Cape Floral kingdom, shellfish, and modern human origins. J. Hum. Evol. 59, 425–443.
Marean, C.W., 2011. Coastal South Africa and the co-evolution of the modern human lineage and the coastal adaptation. In: Bicho, N., Haws, J.A., Davis, L.G. (Eds.), Trekking the Shore: Changing Coastlines and the Antiquity of Coastal Settlement. Springer, New York, pp. 421–440.
Marean, C.W., 2014. The origins and significance of coastal resource use in Africa and Western Eurasia. J. Hum. Evol. 77, 17–40.
Marean, C.W., 2016. The transition to foraging for dense and predictable resources and its impact on the evolution of modern humans. Philos. Trans. R. Soc. B 371, 20150239.
McBrearty, S., Brooks, A.S., 2000. The revolution that wasn't: A new interpretation of the origin of modern human behaviour. J. Hum. Evol. 39, 453–563.
McCall, G.S., 2007. Behavioral ecological models of lithic technological change during the later Middle Stone Age of South Africa. J. Archaeol. Sci. 34, 1738–1751.
McNabb, J., Beaumont, P., 2012. Excavations in the Acheulean levels at the earlier stone age site of canteen koppie, northern province, South Africa. Proc. Prehist. Soc. 78, 51–71.
Mellars, P., 1989. Major issues in the emergence of modern humans. Curr. Anthropol. 30, 349–385.
Mellars, P., 1994. The Upper Paleolithic Revolution. The Oxford Illustrated Prehistory of Europe. Oxford University Press, Oxford, pp. 42–78.
Mellars, P., Stringer, C. (Eds.), 1989. The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Hominids. Edinburgh University Press, Edinburgh.
Mercader, J., 2009. Mozambican grass seed consumption during the Middle Stone Age. Science 326, 1680–1683.
Mesoudi, A., 2011. Cultural Evolution: How Darwinian Theory can Explain Human Culture and Synthesize the Social Sciences. University of Chicago Press, Chicago.
Miller, J.M., Willoughby, P.R., 2014. Radiometrically dated ostrich eggshell beads from the Middle and Later Stone Age of Magubike Rockshelter, southern Tanzania. J. Hum. Evol. 74, 118–122.
Miller, J.M., Wang, Y.V., 2022. Ostrich eggshell beads reveal 50,000-year-old social network in Africa. Nature 601, 234–239.
Mithen, S.J., 1996. The Prehistory of the Mind a Search for the Origins of Art, Religion and Science. Thames and Hudson, London.
Mourre, V., Villa, P., Henshilwood, C., 2010. Early use of pressure flaking on lithic artifacts at Blombos Cave, South Africa. Science 330, 659–662.
Muller, A., Clarkson, C., Shipton, C., 2017. Measuring behavioural and cognitive complexity in lithic technology throughout human evolution. J. Anthropol. Archaeol. 48, 166–180.
Muller, A., Shipton, C., Clarkson, C., 2022. Stone toolmaking difficulty and the evolution of hominin technological skills. Sci. Rep. 12, 1–12.
Muthukrishna, M., Shulman, B.W., Vasilescu, V., Henrich, J., 2013. Sociality influences cultural complexity. Philos. Trans. R. Soc. B 281, 20132511.
Nami, M., Moser, J., 2010. La Grotte d'Ifri n'Ammar; tome 2: Le Paléolithique Moyen. In: Forschungen zur Archäologie Außereuropäischer Kulturen (FAAK) 9. Reichert, Wiesbaden.
Nash, D.J., Coulson, S., Staurset, S., Ullyott, J.S., Babutsi, M., Hopkinson, L., Smith, M.P., 2013. Provenancing of silcrete raw materials indicates long-distance transport to Tsodilo Hills, Botswana, during the Middle Stone Age. J. Hum. Evol. 64, 280–288.
Nash, D.J., Coulson, S., Staurset, S., Ullyott, J.S., Babutsi, M., Smith, M.P., 2016. Going the distance: Mapping mobility in the Kalahari Desert during the Middle Stone Age through multi-site geochemical provenancing of silcrete artefacts. J. Hum. Evol. 96, 113–133.
Niang, K., Blinkhorn, J., Ndiaye, M., 2018. The oldest Stone Age occupation of coastal West Africa and its implications for modern human dispersals: New insight from Tiémassas. Quat. Sci. Rev. 188, 167–173.
Niang, K., Blinkhorn, J., Ndiaye, M., Bateman, M., Seck, B., Sawaré, G., 2020. The Middle Stone Age occupations of Tiémassas, coastal West Africa, between 62 and 25 thousand years ago. J. Archaeol. Sci. Rep. 34, 102658.
Negash, A., Brown, F., Nash, B., 2011. Varieties and sources of artefactual obsidian in the Middle Stone Age of the Middle Awash, Ethiopia. Archaeometry 53, 661–673.
Neubauer, S., Hublin, J.-J., Gunz, P., 2018. The evolution of modern human brain shape. Sci. Adv. 4, eaao5961.
Nowell, A., 2010. Defining behavioral modernity in the context of Neandertal and anatomically modern human populations. Annu. Rev. Anthropol. 39, 437–452.
Ofek, H., 2001. Second Nature: Economic Origins of Human Evolution. Cambridge University Press, Cambridge.
Ossendorf, G., Groos, A.R., Bromm, T., Tekelemariam, M.G., Glaser, B., Lesur, J., Schmidt, J., Akçar, N., Bekele, T., Beldados, A., Demissew, S., Kahsay, T.H., Nash, B.P., Nauss, T., Negash, A., Nemomissa, S., Veit, H., Vogelsang, R., Woldu, Z., Zech, W., Opgenoorth, L., Miehe, G., 2019. Middle Stone Age foragers resided in high elevations of the glaciated Bale Mountains, Ethiopia. Science 365, 583–587.
Parkington, J.E., 2001. Milestones: The impact of systematic exploitation of marine foods on human evolution. In: Tobias, P.V., Raath, M.A., Moggi-Cechi, J., Doyle, G.A. (Eds.), Humanity from African Naissance to Coming Millenia. Firenze University Press, Florence, pp. 327–336.
Parkington, J.E., 2010. Coastal diet, encephalization, and innovative behaviors in the late Middle Stone Age of Southern Africa. In: Cunnane, S.C., Stewart, K.M. (Eds.), Human Brain Evolution—The Influence of Freshwater and Marine Food Resources. Wiley-Blackwell, New Jersey, pp. 189–203.
de la Peña, P., 2015. Refining our understanding of Howiesons Poort lithic technology: The evidence from Grey rocky layer in Sibudu cave (KwaZulu-Natal, South Africa). PLoS One 10, e0143451.
Porraz, G., Negrino, F., 2008. Espaces économiques et approvisionnement minéral au Paléolithique moyen dans l'aire liguro-provençale. Bull. Musée Anthropol. Préhistorique Monaco 1, 29–39.
Porraz, G., Texier, P.-J., Archer, W., Piboule, M., Rigaud, J.-P., Tribolo, C., 2013. Technological successions in the Middle Stone Age sequence of Diepkloof Rock Shelter, Western Cape, South Africa. J. Archaeol. Sci. 40, 3376–3400.
Powell, A., Shennan, S., Thomas, M.G., 2009. Late Pleistocene demography and the appearance of modern human behavior. Science 324, 1298–1301.
Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., Heinze, A., Renaud, G., Sudmant, P.H., de Filippo, C., Li, H., Mallick, S., Dannemann, M., Fu, Q., Kircher, M., Kuhlwilm, M., Lachmann, M., Meyer, M., Ongyerth, M., Siebauer, M., Theunert, C., Tandon, A., Moorjani, P., Pickrell, J., Mullikin, J.C., Vohr, S.H., Green, R.E., Hellmann, I., Johnson, P.L.F., Blanche, H., Cann, H., Kitzman, J.O., Shendure, J., Eichler, E.E., Lein, E.S., Bakken, T.E., Golovanova, L.V., Doronichev, V.B., Shunkov, M.V., Derevianko, A.P., Viola, B., Slatkin, M., Reich, D., Kelso, J., Pääbo, S., 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505, 43–49.
Ramos-Munoz, J., Bernal-Casasola, D., Barrena-Tocini, A., Dominguez-Bella, S., Clemente-Conte, I., Vijande-Vila, E., Cantillo-Duarte, J.J., Almisas-Cruz, S., 2016. Middle Palaeolithic Mode 3 lithic technology in the rock-shelter of Benzú (North Africa) and its immediate environmental relationships. Quat. Int. 413, 21–35.
Raynal, J.P., Sbihi Alaoui, F.Z., Geraads, D., Magoga, L., Mohi, A., 2001. The earliest occupation of North-Africa: The Moroccan perspective. Quat. Int. 75, 65–75.
Raynal, J.P., Sbihi-Alaoui, F.-Z., 2009. Mission Préhistorique et Paléontologique Française "Littoral" Maroc. Rapport sur la Campagne 2009 et Prospective 2010-2011. CNRS, Bordeaux.
Raynal, J.-P., Sbihi-Alaoui, F.-Z., Mohib, A., El Graoui, M., Lefevre, D., Texier, J.-P., Geraads, D., Hublin, J.-J., Smith, T., Tafforeau, P., Zouak, M., Grün, R., Rhodes, E.J., Eggins, S., Daujeard, C., Fernandes, P., Gallotti, R., Hossini, S., Queffelec, A., 2010. Hominid cave at Thomas Quarry I (Casablanca, Morocco): Recent findings and their context. Quat. Int. 223, 369–382.
Richerson, P.J., Boyd, R., 2005. Not by Genes Alone—How Culture Transformed Human Evolution. University of Chicago Press, Chicago.
Richter, D., Moser, J., Nami, M., Eiwanger, J., Mikdad, A., 2010. New chronometric data from Ifri n'Ammar (Morocco) and the chronostratigraphy of the Middle Palaeolithic in the Western Maghreb. J. Hum. Evol. 59, 672–679.
Richter, D., Grün, R., Joannes-Boyau, R., Steele, T.E., Amani, F., Rué, M., Fernandes, P., Raynal, J.-P., Geraads, D., Ben-Ncer, A., Hublin, J.-J., McPherron, S.P., 2017. The age of the hominin fossils from Jebel Irhoud, Morocco, and the origins of the Middle Stone Age. Nature 546, 293–296.
Rightmire, G.P., 2004. Brain size and encephalization in Early to Mid-Pleistocene *Homo*. Am. J. Phys. Anthropol. 124, 109–123.
Robert, A., Soriano, S., Rasse, M., Stokes, S., Huysecom, E., 2003. First chrono-cultural framework for the West African Palaeolithic: New data from Ounjougou, Dogon Country, Mali. J. Afr. Archaeol. 2, 151–169.
Roberts, P., Stewart, B.A., 2018. Defining the 'generalist specialist' niche for Pleistocene *Homo sapiens*. Nat. Hum. Behav. 2, 542–550.
Rodriguez, W., Mazet, O., Grusea, S., Arrendondo, A., Corujo, J.M., Boitard, S., Chikhi, L., 2018. The IICR and the non-stationary structured coalescent: Towards demographic inference with arbitrary changes in population structure. Heredity 121, 663–678.
Rosso, D.E., Pitarch Martí, A., d'Errico, F., 2016. Middle Stone Age ochre processing and behavioural complexity in the Horn of Africa: Evidence from Porc-Epic Cave, Dire Dawa, Ethiopia. PLoS One 11, e0164793.
Rots, V., Van Peer, P., Vermeersch, P.M., 2011. Aspects of tool production, use, and hafting in Palaeolithic assemblages from Northeast Africa. J. Hum. Evol. 60, 637–664.
Rots, V., Lentfer, C., Schmid, V.C., Porraz, G., Conard, N.J., 2017. Pressure flaking to serrate bifacial points for the hunt during the MIS5 at Sibudu Cave (South Africa). PLoS One 12, e0175151.
Ruff, C.B., Trinkaus, E., Holliday, T.W., 1997. Body mass and encephalization in Pleistocene *Homo*. Nature 387, 173–176.
Sackett, J.R., 1990. Style and ethnicity in archaeology: The case for isochrestism. In: Conkey, M.W., Hastorf, C.A. (Eds.), The Uses of Style in Archaeology: Some Historical and Theoretical Issues. Cambridge University Press, Cambridge, pp. 32–43.
Sahle, Y., Braun, D.R., 2018. A reply to Douze and Delagnes's 'The pattern of emergence of a Middle Stone Age tradition at Gademotta and Kulkuletti (Ethiopia) through convergent tool and point technologies' [J. Hum. Evol. 91 (2016) 93–121]. J. Hum. Evol. 125, 201–206.
Sahle, Y., Hutchings, W.K., Braun, D.R., Sealy, J.C., Morgan, L.E., Negash, A., Atnafu, B., 2013. Earliest stone-tipped projectiles from the Ethiopian Rift date to >279,000 years ago. PLoS One 8, e78092.
Scerri, E.M.L., 2012. A new stone tool assemblage revisited: Reconsidering the 'Aterian' in Arabia. Proc. Semin. Arabian Stud. 42, 357–370.
Scerri, E.M.L., 2013a. The Aterian and its place in the North African Middle Stone Age. Quat. Int. 300, 111–130.

Scerri, E.M.L., 2013b. On the spatial and technological organisation of hafting modifications in the North African Middle Stone Age. J. Archaeol. Sci. 40, 4234–4248.
Scerri, E.M.L., 2017a. The North African Middle Stone Age and its place in recent human evolution. Evol. Anthropol. 26, 119–135.
Scerri, E.M.L., 2017b. The West African Stone Age. In: Oxford Research Encyclopedia of African History. http://africanhistory.oxfordre.com/view/10.1093/acrefore/9780190277734.001.0001/acrefore-9780190277734-e-137.
Scerri, E.M.L., Spinapolice, E.E.A., 2019. Lithics of the North African Middle Stone Age. J. Anthropol. Sci. 97, 1–36.
Scerri, E.M.L., Drake, N., Groucutt, H.S., Jennings, R., 2014. Earliest evidence for the structure of *Homo sapiens* populations in Africa. Quat. Sci. Rev. 101, 207–216.
Scerri, E.M.L., Thomas, M.G., Manica, A., Gunz, P., Stock, J., Stringer, C., Grove, M., Groucutt, H.S., Timmermann, A., Rightmire, G.P., d'Errico, F., Tryon, C.A., Drake, N.A., Brooks, A.S., Dennell, R.W., Durbin, R., Henn, B.M., Lee-Thorp, J., deMenocal, P., Petraglia, M.D., Thompson, J.C., Scally, A., Chikhi, L., 2018. Did our species evolve in subdivided populations across Africa, and why does it matter? Trends Ecol. Evol. 33, 582–594.
Scerri, E.M.L., Chikhi, L., Thomas, M.G., 2019. Beyond multiregional and simple out of Africa models of human evolution. Nat. Ecol. Evol. 3, 1370–1372.
Scerri, E.M.L., Blinkhorn, J., Niang, K., Bateman, M., Groucutt, H.S., 2017. Persistence of Middle Stone Age technology to the Pleistocene/Holocene transition supports a complex hominin evolutionary scenario in West Africa. J. Archaeol. Sci. Rep. 11, 639–646.
Scerri, E.M.L., Niang, K., Candy, I., Blinkhorn, J., Mills, W., Cerasoni, J.N., Bateman, M.D., Crowther, A., Groucutt, H.S., 2021. Continuity of the Middle Stone Age into the Holocene. Sci. Rep. 11, 70.
Scerri, E.M.L., Roberts, P., Maezumi, S.Y., Malhi, Y., 2022. Tropical forests in the deep human past. Philos. Trans. R. Soc. B 377, 20200500.
Schick, K., Clark, J.D., 2000. Acheulean archaeology of the Western Middle Awash. In: de Heinzelin, J., Clark, J.D., Schick, K., Gilbert, W.H. (Eds.), The Acheulean and the Plio-Pleistocene Deposits of the Middle Awash Valley, Ethiopia. Musée Royale de l'Afrique Central, Tervuren, pp. 123–181.
Schick, K., Toth, N., 2017. Acheulean industries of the Early and Middle Pleistocene, Middle Awash, Ethiopia. L'Anthropologie 121, 451–491.
Schmid, V.C., Conard, N.J., Texier, P.J., Parkington, J.E., Porraz, G., 2016. The 'MSA 1' of Elands Bay Cave (South Africa) in the context of the southern African Early MSA technologies. South. Afr. Humanit. 29, 153–201.
Schmid, V.C., Porraz, G., Zeidi, M., Conard, N.J., 2019. Blade technology characterizing the MIS 5 DA layers of Sibudu Cave, South Africa. Lithic Technol. 44, 199–236.
Schmid, V.C., Douze, K., Tribolo, C., Lorenzo Martinez, M., Rasse, M., Lespez, L., Lebrun, B., Hérisson, D., Ndiaye, M., Huysecom, E., 2022. Middle Stone Age bifacial technology and pressure flaking at the MIS 3 site of Toumboura III, Eastern Senegal. Afr. Arch. Rev. 39, 1–33.
Schmidt, P., Porraz, G., Slodczyk, A., Bellot-Gurlet, L., Archer, W., Miller, C.E., 2013. Heat treatment in the South African Middle Stone Age: Temperature induced transformations of silcrete and their technological implications. J. Archaeol. Sci. 40, 3519–3531.
Schmidt, P., Mackay, A., 2016. Why was silcrete heat-treated in the Middle Stone Age? An early transformative technology in the context of raw material use at Mertenhof Rock Shelter, South Africa. PLoS One 11, e0149243.
Sealy, J., 2016. Cultural change, demography, and the archaeology of the last 100 kyr in southern Africa. In: Jones, S.A., Stewart, B.A. (Eds.), Africa from MIS 6-2. Springer, Dordrecht, pp. 65–75.
Sehasseh, E.M., Fernandez, P., Kuhn, S., Stiner, M., Mentzer, S., Colarossi, D., Clark, A., Lanoe, F., Pailes, M., Hoffmann, D., Benson, A., Rhodes, E., Benmansour, M., Laissaoui, A., Ziani, I., Vidal-Matutano, P., Morales, J., Djellal, Y., Longet, B., Hublin, J.-J., Mouhiddine, M., Rafi, F.-Z., Worthey, K.B., Sanchez-Morales, I., Ghayati, N., Bouzouggar, A., 2021. Early Middle Stone Age personal ornaments from Bizmoune Cave, Essaouira, Morocco. Sci. Adv. 7, eabi8620.
Shea, J.J., 2008. The Middle Stone Age archaeology of the Lower Omo Valley Kibish Formation: Excavations, lithic assemblages, and inferred patterns of early *Homo sapiens* behavior. J. Hum. Evol. 55, 448–485.
Shea, J.J., 2011. *Homo sapiens* is as *Homo sapiens* was: Behavioural variability versus "behavioural modernity" in Paleolithic archaeology. Curr. Anthropol. 52, 1–35.
Shennan, S., 2001. Demography and cultural innovation: A model and its implications for the emergence of modern human culture. Camb. Archaeol. J. 11, 5–16.
Shipton, C., Roberts, P., Archer, W., Armitage, S.J., Bita, C., Blinkhorn, J., Courtney-Mustaphi, C., Crowther, A., Curtis, R., d'Errico, F., Douka, K., Faulkner, P., Groucutt, H.S., Helm, R., Herries, A.I.R., Jembe, S., Kourampas, N., Lee-Thorp, J., Marchant, R., Mercader, J., Marti, A.P., Prendergast, M.E., Rowson, B., Tengeza, A., Tibesasa, R., White, T.S., Petraglia, M.D., Boivin, N., 2018. 78,000-year-old record of Middle and Later stone age innovation in an East African tropical forest. Nat. Commun. 9, 1832.
Shultz, S., Nelson, E., Dunbar, R.I., 2012. Hominin cognitive evolution: Identifying patterns and processes in the fossil and archaeological record. Philos. Trans. R. Soc. B 367, 2130–2140.
Sievers, C., Backwell, L., d'Errico, F., Wadley, L., 2022. Plant bedding construction between 60,000 and 40,000 years ago at Border Cave, South Africa. Quat. Sci. Rev. 275, 107280.
Sikora, M., Seguin-Orlando, A., Sousa, V.C., Albrechtsen, A., Korneliussen, T., Ko, A., Rasmussen, S., Dupanloup, I., Nigst, P.R., Bosch, M.D., Renaud, G., Allentoft, M.E., Margaryan, A., Vasilyev, S.V., Veselovskaya, E.V., Borutskaya, S.B., Deviese, T., Comeskey, D., Higham, T., Manica, A., Foley, R., Meltzer, D.J., Nielsen, R., Excoffier, L., Mirazon Lahr, M., Orlando, L., Willerslev, E., 2017. Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers. Science 358, 659–662.
Soriano, S., Rasse, M., Tribolo, C., Huysecom, E., 2010. Ounjougou: A long Middle Stone Age sequence in Dogon county (Mali). In: Allsworth-Jones, P. (Ed.), West African Archaeology: New Developments, New Perspectives. BAR International Series, Oxford, pp. 1–14.
Spinapolice, E.A.A., 2012. Raw material economy in Salento (Apulia, Italy): New perspectives on Neanderthal mobility patterns. J. Archaeol. Sci. 39, 680–689.
Spinapolice, E.E., 2020. Lithic variability and cultures in the East African Middle Stone Age. In: Groucutt, H.S. (Ed.), Culture History and Convergent Evolution. Springer, Cham, pp. 87–102.
Steele, T.E., Álvarez-Fernández, E., 2011. Initial investigations into the exploitation of coastal resources in North Africa during the Late Pleistocene at Grotte des Contrebandiers, Morocco. In: Bicho, N., Haws, J.A., Davis, L.G. (Eds.), Trekking the Shore. Springer, New York, pp. 383–403.
Steele, T.E., Mackay, A., Fitzsimmons, K.E., Igreja, M., Marwick, B., Orton, J., Schwortz, S., Stahlschmidt, M.C., 2016. Varsche Rivier 003: A Middle and Later Stone Age site with Still Bay and Howieson's Poort assemblages in southern Namaqualand, South Africa. PaleoAnthropology 2016, 100–163.
Steele, T.E., Álvarez-Fernández, E., Hallett-Desguez, E., 2019. A review of shells as personal ornamentation during the African Middle Stone Age. PaleoAnthropology 2019, 24–51.
Stewart, B.A., Zhao, Y., Mitchell, P.J., Dewar, G., Gleason, J.D., Blum, J.D., 2020. Ostrich eggshell bead strontium isotopes reveal persistent macroscale social networking across late Quaternary southern Africa. Proc. Natl. Acad. Sci. USA 117, 6453–6462.
Stoetzel, E., Campmas, E., Michel, P., Bougariane, B., Ouchaou, B., Amani, F., El Hajraoui, M.A., Nespoulet, R., 2014. Context of modern human occupations in North Africa: Contribution of the Témara caves data. Quat. Int. 320, 143–161.
Stolarczyk, R.E., Schmidt, P., 2018. Is early silcrete heat treatment a new behavioural proxy in the Middle Stone Age? PLoS One 13, e0204705.
Strassberg, S.S., Creanza, N., 2021. Cultural evolution and prehistoric demography. Philos. Trans. R. Soc. B 376, 20190713.
Straus, L.G., 1996. Continuity or rupture; convergence or invasion; adaptation or catastrophe; mosaic or monolith: Views on the Middle to Upper Paleolithic transition in Iberia. In: Carbonell, E., Vaquero, M. (Eds.), The Last Neanderthals, the First Anatomically Modern Humans. Cultural Change and Human Evolution: The Crisis at 40 ka BP. Universitat Rovira i Virgili, Tarragona, pp. 203–218.
Stringer, C., Andrews, P., 1988. Genetic and fossil evidence for the origin of modern humans. Science 239, 1263–1268.
Stringer, C., 2002. Modern human origins: Progress and prospects. Philos. Trans. R. Soc. B 357, 563–579.
Taylor, N., 2022. Riddles wrapped inside an enigma. Lupemban MSA technology as a rainforest adaptation: Revisiting the lanceolate point. Philos. Trans. R. Soc. B 377, 20200484.
Tennie, C., Call, J., Tomasello, M., 2009. Ratcheting up the ratchet: On the evolution of cumulative culture. Philos. Trans. R. Soc. B 364, 2405–2415.
Texier, P.J., Porraz, G., Parkington, J., Rigaud, J.-P., Poggenpoel, C., Miller, C., Tribolo, C., Cartwright, C., Coudenneau, A., Klein, R., Steele, T., Verna, C., 2010. A Howiesons Poort tradition of engraving ostrich eggshell containers dated to 60,000 years ago at Diepkloof Rock Shelter, South Africa. Proc. Natl. Acad. Sci. USA 107, 6180–6185.
Texier, P.-J., Porraz, G., Parkington, J.E., Rigaud, J.-P., Poggenpoel, C.E., Tribolo, C., 2013. The context, form and significance of the MSA engraved ostrich eggshell collection from Diepkloof Rock Shelter, Western Cape, South Africa. J. Archaeol. Sci. 40, 3412–3431.
Thompson, J.C., Mackay, A., Nightingale, S., Wright, D., Choi, J.H., Welling, M., Blackmore, H., Gomani-Chindebvu, E., 2018. Ecological risk, demography and technological complexity in the Late Pleistocene of northern Malawi: Implications for geographical patterning in the Middle Stone Age. J. Quat. Sci 33, 261–284.
Thompson, J.C., Wright, D.K., Ivory, S.J., Choi, J.H., Nightingale, S., Mackay, A., Schilt, F., Otárola-Castillo, E., Mercader, J., Forman, S.L., Pietsch, T., Cohen, A.S., Arrowsmith, J.R., Welling, M., Davis, J., Schiery, B., Kaliba, P., Malijani, O., Blome, M.W., O'Driscoll, C.A., Mentzer, S.M., Miller, C., Heo, S., Choi, J., Tembo, J., Mapemba, F., Simengwa, D., Gomani-Chindebvu, E., 2021. Early human impacts and ecosystem reorganization in southern-central Africa. Sci. Adv. 7, eabf9776.
Tomasso, S., Rots, V., 2018. What is the use of shaping a tang? Tool use and hafting of tanged tools in the Aterian of Northern Africa. Archaeol. Anthropol. Sci. 10, 1389–1417.
de la Torre, I., Mora, R., Arroyo, A., Benito-Calvo, A., 2014. Acheulean technological behaviour in the Middle Pleistocene landscape of Mieso (East-Central Ethiopia). J. Hum. Evol. 76, 1–25.
Tostevin, G.B., 2012. Seeing Lithics: A Middle-Range Theory for Testing for Cultural Transmission in the Pleistocene. Oxbow Books, Oxford.
Tryon, C.A., McBrearty, S., 2002. Tephrostratigraphy and the Acheulian to Middle Stone Age transition in the Kapthurin Formation, Kenya. J. Hum. Evol. 42, 211–235.
Tryon, C.A., McBrearty, S., Texier, P.J., 2005. Levallois lithic technology from the Kapthurin Formation, Kenya: Acheulian origin and Middle Stone Age diversity. Afr. Archaeol. Rev. 22, 199–229.
Tryon, C.A., Faith, J.T., 2013. Variability in the Middle Stone Age of Eastern Africa. Curr. Anthropol. 54, 234–254.

Tryon, C.A., Faith, J.T., 2016. A demographic perspective on the Middle to Later Stone Age transition from Nasera rockshelter, Tanzania. Philos. Trans. R. Soc. B 371, 20150238.
Tryon, C.A., Lewis, J.E., Ranhorn, K.L., Kwekason, A., Alex, B., Laird, M.F., Marean, C.W., Niespolo, E., Nivens, J., Mabulla, A.Z.P., 2018. Middle and Later Stone Age chronology of Kisese II rockshelter (UNESCO World Heritage Kondoa Rock-Art Sites), Tanzania. PLoS One 13, e0192029.
United Nations, 2019. Standard country or area codes for statistical use (M49).
Vaesen, K., Scherjon, F., Hemerik, L., Verpoorte, A., 2019. Inbreeding, Allee effects and stochasticity might be sufficient to account for Neanderthal extinction. PLoS One 14, e0225117.
Van Peer, P., Fullagar, R., Stokes, S., Bailey, R.M., Moeyersons, J., Steenhoudt, F., Geerts, A., Vanderbeken, T., de Dapper, M., Geus, F., 2003. The Early to Middle Stone Age transition and the emergence of modern human behaviour at site 8-B-11, Sai Island, Sudan. J. Hum. Evol. 45, 187–193.
Van Peer, P., Vermeersch, P.M., Paulissen, E., 2010. Taramsa 1: Chert Quarrying, Lithic Technology and a Human Burial at the Palaeolithic site of Taramsa 1, Upper Egypt. Leuven University Press, Leuven.
Vanhaeren, M., d'Errico, F., Stringer, C., James, S.L., Todd, J.A., Mienis, H.K., 2006. Middle Paleolithic shell beads in Israel and Algeria. Science 312, 1785–1788.
Vanhaeren, M., d'Errico, F., Van Niekerk, K.L., Henshilwood, C.S., Erasmus, R.M., 2013. Thinking strings: Additional evidence for personal ornament use in the Middle Stone Age at Blombos Cave, South Africa. J. Hum. Evol. 64, 500–517.
Vaquero, M., Vallverdú, J., Rosell, J., Pastó, I., Allué, E., 2001. Neandertal behavior at the Middle Palaeolithic Site of Abric Romaní, Capellades, Spain. J. Field Archaeol. 28, 93–114.
Villa, P., Roebroeks, W., 2014. Neandertal demise: An archaeological analysis of the modern human superiority complex. PLoS One 9, e96424.
Villa, P., Soressi, M., Henshilwood, C., Mourre, V., 2009. The Still Bay points of Blombos Cave (South Africa). J. Archaeol. Sci. 36, 441–460.
Vogelsang, R., Richter, J., Jacobs, Z., Eichhorn, B., Linseele, V., Roberts, R.G., 2010. New excavations of Middle Stone Age deposits at Apollo 11 Rockshelter, Namibia: Stratigraphy, archaeology, chronology and past environments. J. Afr. Archaeol. 8, 185–218.
Wadley, L., 2001. What is cultural modernity? A general view and a South African perspective from Rose Cottage Cave. Cam. Archaeol. J. 11, 201–221.
Wadley, L., 2013. Recognizing complex cognition through innovative technology in Stone Age and Palaeolithic sites. Camb. Archaeol. J. 23, 163–183.
Wadley, L., 2015. Those marvellous millennia: The Middle Stone Age of southern Africa. Azania 50, 155–226.
Wadley, L., 2021. What stimulated rapid, cumulative innovation after 100,000 years ago? J. Archaeol. Method Theory 28, 120–141.
Wadley, L., Hodgskiss, T., Grant, M., 2009. Implications for complex cognition from the hafting of tools with compound adhesives in the Middle Stone Age, South Africa. Proc. Natl. Acad. Sci. USA 106, 9590–9594.
Wadley, L., Sievers, C., Bamford, M., Goldberg, P., Berna, F., Miller, C., 2011. Middle Stone Age bedding construction and settlement patterns at Sibudu, South Africa. Science 334, 1388–1391.
Wadley, L., Backwell, L., d'Errico, F., Sievers, C., 2020a. Cooked starchy rhizomes in Africa 170 thousand years ago. Science 367, 87–91.
Wadley, L., Esteban, I., De La Peña, P., Wojcieszak, M., Stratford, D., Lennox, S., d'Errico, F., Rosso, D.E., Orange, F., Backwell, L., Sievers, C., 2020b. Fire and grass-bedding construction 200 thousand years ago at Border Cave, South Africa. Science 369, 863–866.
Wang, K., Mathieson, I., O'Connell, J., Schiffels, S., 2020. Tracking human population structure through time from whole genome sequences. PLoS Genet. 16, e1008552.
Watts, I., 2010. The pigments from Pinnacle Point Cave 13B, Western Cape, South Africa. J. Hum. Evol. 59, 392–411.
Watts, I., Chazan, M., Wilkins, J., 2016. Early evidence for brilliant ritualized display: Specularite use in the Northern Cape (South Africa) between ~500 and ~300 ka. Curr. Anthropol. 57, 287–310.
Way, A.M., de la Peña, P., de la Peña, E., Wadley, L., 2022. Howiesons Poort backed artifacts provide evidence for social connectivity across southern Africa during the Final Pleistocene. Sci. Rep. 12, 1–12.
Wells, J.C.K., Stock, J.T., 2007. The biology of the colonizing ape. Yearb. Phys. Anthropol. 50, 191–222.
Wiessner, P., 1983. Style and social information in Kalahari San projectile points. Am. Antiq. 48, 253–276.
Wiessner, P., 1997. Seeking guidelines through an evolutionary approach: Style revisited among the!Kung San (Ju/'hoansi) of the 1990s. In: Barton, M., Clark, G. (Eds.), Rediscovering Darwin: Evolutionary Theory and Archaeological Explanation. Archaeological Publications of the AAA Monograph Series, Washington D.C, pp. 157–176.
White, T.D., Asfaw, B., DeGusta, D., Gilbert, H., Richards, G.D., Suwa, G., Howell, F.C., 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. Nature 423, 742–747.
Wilkins, J., Chazan, M., 2012. Blade production ~500 thousand years ago at Kathu Pan 1, South Africa: Support for a multiple origins hypothesis for early Middle Pleistocene blade technologies. J. Archaeol. Sci. 39, 1883–1900.
Wilkins, J., Schoville, B.J., Brown, K.S., Chazan, M., 2012. Evidence for early hafted hunting technology. Science 338, 942–946.
Wilkins, J., Schoville, B.J., Pickering, R., Gliganic, L., Collins, B., Brown, K.S., von der Meden, J., Khumalo, W., Meyer, M.C., Maape, S., Blackwood, A.F., Hatton, A., 2021. Innovative *Homo sapiens* behaviours 105,000 years ago in a wetter Kalahari. Nature 592, 248–252.
Will, M., Conard, N.J., 2018. Assemblage variability and bifacial points in the lowermost Sibudan layers at Sibudu, South Africa. Archaeol. Anthropol. Sci. 10, 389–414.
Will, M., Mackay, A., 2017. What factors govern the procurement and use of silcrete during the Stone Age of South Africa? J. Archaeol. Sci. Rep. 15, 630–645.
Will, M., Bader, G.D., Conard, N.J., 2014. Characterizing the Late Pleistocene MSA lithic technology of Sibudu, KwaZulu-Natal, South Africa. PLoS One 9, e98359.
Will, M., Conard, N.J., Tryon, C.A., 2019a. Timing and trajectory of cultural evolution on the African continent 200,000-30,000 years ago. In: Sahle, Y., Reyes-Centeno, H., Bentz, C. (Eds.), Modern Human Origins and Dispersal. Kerns Verlag, Tübingen, pp. 25–72.
Will, M., Kandel, A.W., Conard, N.J., 2019b. Midden or molehill: The role of coastal adaptations for human evolution and dispersal. J. World Prehist. 32, 33–72.
Wright, S., 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. In: Proceedings of the Sixth International Congress on Genetics, vol. 1, pp. 356–366.
Wright, S., 1982. The shifting balance theory and macroevolution. Annu. Rev. Genet. 16, 1–19.
Wurz, S., 1999. The Howiesons Poort backed artefacts from Klasies River: An argument for symbolic behaviour. S. Afr. Archaeol. Bull. 1999, 38–50.
Wurz, S., 2002. Variability in the Middle Stone Age lithic sequence, 115,000–60,000 years ago at Klasies river, South Africa. J. Archaeol. Sci. 29, 1001–1015.
Wurz, S., 2013. Technological trends in the Middle Stone Age of South Africa between MIS 7 and MIS 3. Curr. Anthropol. 54, 305–319.
Wurz, S., 2014. Southern and east African Middle Stone Age: Geography and culture. In: Smith, C. (Ed.), Encyclopedia of Global Archaeology. Springer, New York, pp. 6890–6912.
Wynn, T., Coolidge, F., 2008. Why not cognition? Curr. Anthropol. 49, 895–897.
Wynn, T., Overmann, K.A., Coolidge, F.L., 2016. The false dichotomy: A refutation of the Neandertal indistinguishability claim. J. Anthropol. Sci. 94, 1–22.
Zaidner, Y., Weinstein-Evron, M., 2016. The end of the Lower Paleolithic in the Levant: The Acheulo-Yabrudian lithic technology at Misliya Cave, Israel. Quat. Int. 409, 9–22.
Zilhão, J., 2007. The emergence of ornaments and art: An archaeological perspective on the origins of "behavioural modernity". J. Archaeol. Res. 15, 1–54.
Ziegler, M., Simon, M.H., Hall, I.R., Barker, S., Stringer, C., Zahn, R., 2013. Development of Middle Stone Age innovation linked to rapid climate change. Nat. Commun. 4, 1905.
Zollikofer, C.P., Bienvenu, T., Beyene, Y., Suwa, G., Asfaw, B., White, T.D., Ponce de León, M.S., 2022. Endocranial ontogeny and evolution in early *Homo sapiens*: The evidence from Herto, Ethiopia. Proc. Natl. Acad. Sci. USA 119, e2123553119.