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Chapter 2

Timing and trajectory of cultural evolution on the African continent 200,000-30,000 years ago

Manuel Will[a,b,c], *Nicholas J. Conard*[a,d], *Christian A. Tryon*[e]

"…commence with the local and provincial and proceed to the areal and regional." F. Clark in Howell (1967: 903)

"…grand narratives are currently on hold, universal statements should be treated with caution, and local rather than global is currently king." Clive Gamble in Henshilwood and Marean (2003: 639)

Abstract

The period from 200,000 to 30,000 years ago in Africa encompasses the archaeological background for the early evolution and global dispersal of *Homo sapiens*. Here we provide an overview of current models of behavioral change and cultural evolution in this timeframe, followed by a review on the timing and temporal trajectory of relevant empirical data in Africa. Because recent anthropological and genetic work has highlighted the importance of structure within ancient populations of Africa, we adopt a geographically explicit perspective. We emphasize comparisons between the archaeological records of southern, northern, eastern, central and western Africa, recognizing the varying geological and environmental backgrounds, political circumstances, and histories of research across the continent. Our review finds different records and temporal trajectories for complex material culture and behavioral innovations among the African regions, with the earliest evidence for many cultural changes already present during the late Middle Pleistocene in all areas. The bulk of the evidence, however, comes from Marine Isotope Stages (MIS) 5-3, a period characterized by complex temporal trajectories and spatial differences among and within regions. Prominent models for a late emergence of sophisticated behaviors at ~50,000 years ago or a gradual and cumulative evolution of cultural complexity in all of Africa are not supported. In light of these results, we advocate abandoning continent-wide, directional and unilinear models of cultural change in favor of more highly contextualized, temporally variable, and historically contingent trajectories in different regions, encapsulated in the concept of complex landscapes of cultural evolution.

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INTRODUCTION

For over two decades, the biological origins of *Homo sapiens* have been firmly placed in space and time, with human fossils and genetic information suggesting sub-Saharan, and most likely eastern, Africa, around 200,000–150,000 years before present (=200–150 ka; Cann et al. 1987; Stringer and Andrews 1988; Bräuer 1992; White et al. 2003; McDougall et al. 2005). Yet in the past five years, several challenges have arisen to this scenario. Skeletal remains interpreted by some as the earliest members of our species from north of the Sahara at Jebel Irhoud have been dated to ~300 ka (Hublin et al. 2017; Richter et al. 2017). Genomic studies have provided a more diffuse picture for the geographical origin of *H. sapiens* based on large samples of modern DNA and increasing amounts of aDNA from Africa (Mallick et al. 2016; Schlebusch et al. 2017; Skoglund et al. 2017; van de Loosdrecht et al. 2018). New models emerging from these findings emphasize multiple origins for our species within Africa—"pan-African" (Hublin et al. 2017) or "African multiregionalism" (Stringer 2016)—with a strong signal of ancient population substructure and marked anatomical diversity until the end of the Pleistocene (Gunz et al. 2009; Harvati et al. 2011; Tryon et al. 2015; Crevecoeur et al. 2016; Lahr 2016; Scerri et al. 2018). Recent archaeological research in Africa has likewise emphasized high levels of metapopulation structure (Scerri et al. 2014) and persisting "archaic" elements in lithic technology (e.g., Scerri et al. 2017; Leplongeon et al. 2018; Scerri et al. 2018). These developments exemplify the vitality of current research into the origins of *H. sapiens*. Moreover, parallels can be found in the changing history of thought on the cultural evolution of our species in the recent past, which lies at the heart of this contribution.

In the late 1980s and early 1990s, the dominant "Human Revolution" paradigm for the cultural evolution of *H. sapiens* (e.g., Mellars and Stringer 1989; Bar-Yosef 2002) posited a relatively sudden emergence of cultural complexity (e.g., language, symbolic behavior) in our species at about 40 ka in Europe, coinciding with the earliest arrival of modern humans to that continent. With the growing consensus that the early biological evolution of our species took place much earlier in Africa (Cann et al. 1987; Stringer and Andrews 1988; Bräuer 1992), archaeological research gradually shifted to the Middle Stone Age (MSA) dating to ~300-30 ka, in search for the material cultural background around the origin of *H. sapiens*. Before, there had been little intrinsic interest in this period, with the scarcity of faunal remains and lack of reliable dating methods further impeding research (Robertshaw 1995; Conard et al. 2014; Wadley 2015). Beginning in the late 1990s, the MSA yielded archaeological finds with unexpectedly early dates that were previously associated only with the European Upper Paleolithic, including abstract depictions, personal ornaments, and bone artifacts. Eventually, the African continent replaced Europe as the center of attention for studying the early cultural evolution of modern humans (Brooks et al. 1995; Yellen et al. 1995; Foley and Lahr 1997; McBrearty and Brooks 2000; Klein 2001; Wadley 2001; Henshilwood and Marean 2003; Mellars 2006; but see Conard 2005; 2008; 2010a). This reorientation in research focus has led to the formulation of new models for the behavioral evolution of our species with a focus on the African evidence.

The goals of this paper are threefold: First, we provide an overview of some of the different models for the cultural evolution of *H. sapiens* and their empirical expectations. Second, we review the spatial and temporal variability of selected aspects of material culture in the African record during 200-30 ka, consistent with the later two thirds of the period in which MSA sites occur. We emphasize the need for a spatially explicit perspective to account for different geographical areas in Africa, and discuss issues of scale and the comparability of the regional records which come with this approach. Third, we synthesize the overall pattern of cultural change during 200-30 ka and test different theoretical models against this empirical baseline. Our hope is to further current debates on the origins and evolution of modern humans, illustrate the complexity of the issue and provide some thoughts on future ways to increase our understanding. In this final discussion we also touch upon issues of causality and potential implications for population substructure.

MODELS FOR THE CULTURAL EVOLUTION OF *HOMO SAPIENS*

When and where did humans become like us in their behavior, culture and cognition? How did these capacities evolve? While these issues are paramount for archaeology, anthropology and beyond, they are still highly debated. We do not intend to get lost in semantic discussions surrounding terms such as "cultural modernity," which has frequently implied the existence of a certain threshold based on a trait list approach (see for discussion Wadley 2001; Henshilwood and Marean 2003; Conard 2008; Shea 2011; Wynn et al. 2016). Instead we pursue an empirically driven approach on the timing and temporal trajectory of the appearance in different regions of specific innovations and new artifact categories that are considered as indicators of complex behaviors and advanced cognition (e.g., increased long-term problem solving and working memory) that need not be unique to a particular taxon.

Researchers have developed various models for the cultural and behavioral evolution of modern humans during the last 20 years, based on the MSA archaeological record (~300-30 ka) which broadly coincides with the biological origin and early evolution of our species. The models differ with regards to the trajectory and timing of behavioral change, causal mechanisms, geographical focus, and overall scope. We briefly summarize five models, though more have been proposed (see also summary in Table 1):

1) McBrearty and Brooks (2000) suggest a long, gradual and cumulative cultural evolution for *H. sapiens* within Africa, following a

stepwise process that started around their biological origin at 200–150 ka. Their assessment is based on an extensive review of the archaeological data present in 2000. This model uses 'Africa' as the basic analytical unit, effectively treating *H. sapiens* across the continent as a single connected population.

2) Klein (1994, 2000, 2008, 2009) favors a sudden origin of behavioral modernity within Africa at a late point around ~50–40 ka coincident with the origin of the Later Stone Age (LSA) and a marked increase in material complexity. This process is initiated by a genetic mutation causing neurological changes (e.g., language) which prompted a flourishing of behavioral innovations. This mutation arose once (in a single population) but subsequently spread throughout other groups by its selective advantages. Although not specified in the model, this spread requires either a series of interconnected groups or population dispersal.
3) Two models argue for an association of the evolution of complex culture with an increasing use of marine food resources within the African coastal zone. For Parkington (2001, 2003, 2010), the high concentration of brain-specific nutrients in these resources led to larger brains and increased cognitive functions from MIS 5 (~130–74 ka) onward in a gradual fashion, laying the neurological groundwork for the increasing complexity seen in the archaeological record of southern Africa in the Late Pleistocene. Marean (2011, 2015, 2016) links the evolution of advanced cognition and

Table 1.
Main characteristics of selected models for the cultural evolution of *Homo sapiens* in Africa.

Model	Timing[1]	Trajectory	Region	Causality	Reference
Gradual and cumulative	Late MP (MIS 7-6)	Unidirectional and accretionary	Africa	Not specified	McBrearty and Brooks (2000)
Sudden origin LSA	LP (~50-40 ka)	Abrupt and step-change	Africa	Genetic mutation (neurology/language)	Klein (1994, 2000, 2001, 2008)
Coastal complexity 1 / 2	LP (MIS 5) / Late MP (MIS 6)	Gradual and cumulative / Step-change	Africa (coasts)	Coastal adaptations (brain-specific nutrients / dense resource foraging)	1) Parkington (2001, 2003, 2010) / 2) Marean (2015, 2016)
'Synthetic Model'	LP (~77-70 and 64-58 ka)	Discontinuous and abrupt	South Africa	Demography	Jacobs et al. (2008); Jacobs and Roberts (2008); Henshilwood and Dubreuil (2011)
Mosaic Polycentric Modernity	Late MP – LP (regionally different)	Decentralized, heterogenic and multidirectional	Global	Not specified; regionally and historically contingent	Conard (2005, 2007, 2008, 2010a)

[1] Earliest evidence for increased cultural complexity in *Homo sapiens*. MP = Middle Pleistocene; LP = Late Pleistocene.

increased sociality to Late Pleistocene climatic shifts beginning in MIS 6, with some groups focusing on dense, predictable coastal resources which in turn triggered major changes in territoriality, formation of ethnolinguistic groups, and navigating complex social relationships via material culture. Many of these behaviors are then assumed to spread across the rest of the continent (see Will et al. 2019 for more detailed discussion).

4) The 'Synthetic Model' (e.g., Jacobs et al. 2008; Jacobs and Roberts 2008, 2009; Henshilwood and Dubreuil 2011; see discussion in Conard et al. 2014) focuses on the rich southern Africa record. It maintains that the early behavioral evolution of *H. sapiens* in this region is characterized by abrupt and discontinuous cultural change, materialized by two short and disconnected periods of exceptional cultural innovation and complexity in MIS 4, followed and preceded by less sophisticated phases. These changes are explained primarily by demographic fluctuations, with increasing social connectivity leading to enhanced cultural complexity, and a subsequent spread of these elements to the north (see also Mellars 2006; Mellars et al. 2013). The relation of the model to the rest of Africa is unclear.
5) Conard (2005, 2008, 2010a, 2013) suggests a model of "Mosaic Polycentric Modernity", rejecting the idea of a monogenetic origin in Africa. The model instead favors a decentralized, heterogenic, and multi-origin pattern on a global scale. It emphasizes historical contingency, with "modern" forms of behavior occurring at different times in different environmental, social and economic contexts. This model assumes equal cognitive and behavioral capacities among widespread populations.

Despite their dissimilarities, the models above set out clear hypotheses and predictions on patterns of cultural evolution in *H. sapiens*. We thus empirically test these scenarios by an up-to-date review of the 200-30 ka archaeological record. While not seeking to rival the scope of McBrearty and Brooks (2000), we emphasize new data from the last 15 years and major diachronic trends in different regions of Africa.

THE AFRICAN RECORD DURING 200-30 KA: SPATIAL AND TEMPORAL VARIABILITY IN MATERIAL CULTURE

Methodological considerations

At >30 million square kilometers—a fifth of the world's landmass—Africa is enormous and topographically and environmentally complex. We thus believe that treating Africa as a single analytical unit does not represent a useful starting point. In addition, beginning by about 300 ka, post-Acheulian sites in Africa and Eurasia are characterized by a degree of regional variability greater than that seen before. We therefore adopt as our null hypothesis that each African region will have its own archaeological trajectory, which can be tested by comparing the different records. The need for such a geographically explicit perspective is in line with recent anthropological and genetic work highlighting spatial and temporal structuring within ancient populations of humans in Africa (see also d'Errico and Banks 2013; Scerri 2017a). Furthermore, we assume that the extent to which different regions appear similar or dissimilar is mediated at least in part by (a) archaeological research intensity, (b) differences between taxonomic or analytical systems, and (c) differences in local geology and environments. As its basis, the review thus takes a comparative perspective among different regions, splitting the continent into southern, eastern, northern, central plus western Africa as analytical units, following the United Nations geoscheme with some minor changes (see Fig. 1) well aware of the limitations of this choice and the feasibility of other divisions.

Based on this partitioning, we review the main trajectories and temporal variability in selected behavioral innovations and elements of material culture of the archaeological record for each region during ~200-30 ka. To this end, the presentation of evidence is structured by Marine

Fig. 1.
Geographical map of Africa with analytical units in different colors.

Isotope Stages (MIS) as organizing tools (MIS 6: 190-131 ka; MIS 5: 130-71 ka; MIS 4: 70-60 ka; MIS 3: 59-29 ka), cognizant of the problems with this approach within Africa (e.g., Blome et al. 2012). We chose this timeframe and structure to place the African record in the context of global prehistory of *H. sapiens* prior to the onset of the Late Glacial Maximum and to sidestep terminological issues associated with usage of the terms MSA and LSA, particularly at their interface. With regard to our lower age boundary, more than one species of *Homo* is known in Africa between 300-200 ka, whereas the archaeology of MIS 6-3 is more firmly associated with fossils of *H. sapiens*, albeit with marked morphological variability (McBrearty and Brooks 2000; Dusseldorp et al. 2013; Grine 2016; Lahr 2016; Dirks et al. 2017). A full review of empirical data is beyond the scope of this paper. Instead we focus on the spatial and temporal distribution of selected elements of material culture and behavioral innovations by African region that are commonly interpreted to reflect advanced technological skills, higher cognitive function, and increased social complexity. We chose lithic (bifacial/tanged and backed pieces) and non-lithic elements (beads, bone tools, ochre/colorants, abstract designs) as well as further behavioral traits (hafting, coastal foraging, long-distance movement of raw material) which feature prominently in current discussions, providing a comparable baseline (e.g., McBrearty and Brooks, 2000; Henshilwood and Marean 2003; Henshilwood and Dubreuil 2011; Conard 2013; Perreault et al. 2013; Wadley 2015; Brooks et al. 2018).

As noted above, there are important issues concerning comparability between regions: the African continent hosts an immense diversity of climates, biomes and geological substrates. Due to its tremendous size, considerable topographic variation, a marked north-south geographical long axis and the resulting combination of various climatic factors, Africa's ecological zones include rainforests in the center and west, mangrove forests on the coast all the way to savannahs, grasslands, semi-arid regions and true deserts. Important geological and geographical differences include high mountain ranges (some glaciated), highlands, the rugged terrain of the Rift Valley, vast open plains, long and diverse coastlines, major rivers and lakes but also areas devoid of large water sources.

Geological differences further dictate the presence of often different kinds of rock being present in the various regions of the continent, with the effects of divergent qualities of raw materials on lithic technology being well-documented. Whereas volcanic and often finer-grained rocks dominate parts of eastern Africa (i.e., obsidian), a scarcity of alternative lithic materials prevails in the rainforests of Equatorial Africa where non-conchoidally fracturing quartz was used. Geology also has an impact on archaeological site types: The southern and northwestern African MSA record derives largely from deep cave and rock-shelter sequences with long stratigraphies, enabling detailed diachronic observations. In contrast, central and most of eastern Africa possess a greater number of open-air sites that have more spatial control but shorter temporal sequences. These differences impact both the preservation of archaeological material and influence the way of archaeological research (i.e., landscape and 'off-site' archaeology in eastern Africa vs. site-based work in southern Africa).

Alongside environmental and geological situations, political-historical circumstances and research traditions differ significantly between the regions (for overviews see papers in Robertshaw 1990; Mitchell and Lane 2013). Access to southern, northwestern and eastern African was comparatively easier for international research teams, with a more stable infrastructure and established local research institutions. Western, and some parts of central Africa received far less scholarly research focused on sites >40 ka, due to a combination of more challenging political, environmental and geological situations. On top of this, the fragmented colonial history of the African continent has left its stamp in the divergent approaches to artefact analysis and fieldwork as well as the type and language of publication between geographical regions (e.g., French archaeology in northern Africa vs. Anglo-Saxon research in eastern Africa). There is a long history of regionally specific taxonomies and nomenclatures for individual stone tools and cultural units in the African Stone Age used by local researchers that renders inter-regional comparisons difficult (see, e.g., Lombard et al. 2012; Scerri 2017a).

All of the above factors must be considered when interpreting patterns resulting from our comparative review of the African archaeological record with the goal of exposing inter-regional similarities and differences during ~200-30 ka. Our assessment also highlights potentials and problems of the current record for assessing the trajectory and causes of cultural evolution in early *H. sapiens*. The scale for this review is at a high level (regional and multi-millennial) according to the goals of this contribution, with the downside effect that subtle but important variability from smaller areas and individual sites is neglected. For a richer assessment of individual regions, we refer the reader to recent detailed reviews for southern (Lombard et al. 2012; Wurz 2013; Mackay et al. 2014; Wadley 2015), central (Mercader and Martí 2002; Taylor 2011, 2014, 2016; Cornelissen 2016), eastern (Basell 2008; Tryon and Faith 2013; Lahr and Foley 2016; Blinkhorn and Grove 2018), northern (Van Peer and Vermeersch 2007; Barton and d'Errico 2012; Linstädter et al. 2012; Dibble et al. 2013; Van Peer 2016; Scerri 2017a; Campmas 2018) and western Africa (Taylor 2014; Scerri 2017b; Chevrier et al. 2018). In the following, the archaeological record of each region will first be introduced from a general perspective—encompassing research history, spatiotemporal structure and nomenclature—followed by a review of complex elements of material cultural and behavioral innovations structured by MIS stages within ~200-30 ka.

Southern Africa

The Late Pleistocene record of southern Africa (Fig. 1) has been a focus of research since the late 1990s, due to the recovery of spectacular and early finds, and increased numbers of international research teams after the end of Apartheid. This region has a long research history (e.g., Goodwin and van Riet Lowe 1929) and thus dozens of excavated sites. Due to the good preservation of organic material, southern Africa harbors the best information on subsistence strategies, providing important additional data on cultural and behavioral capacities. Geological circumstances led to the formation of numerous sheltered localities that attracted people but also acted as sediment traps conducive to the accumulation of cultural materials. The formation of such deep stratigraphies at prominent sites like Klasies River, Blombos, Diepkloof, Pinnacle Point, Sibudu or Apollo 11 provides thick archaeological sequences and frequent preservation of organic remains. Work often takes a diachronic perspective, leading to the development of supra-regional cultural stratigraphies (e.g., Goodwin and van Riet Lowe 1929, Volman 1981; Singer and Wymer 1982; Wurz 2002; Lombard et al. 2012), with a recent focus on the Howiesons Poort (HP) and Still Bay (SB) during MIS 4 (e.g., Jacobs et al. 2008; Henshilwood 2012). Geographically, most research has been done on the South African coastlines (particularly the Western Cape), whereas inland South Africa as well as Namibia, Mozambique, Zimbabwe have received less attention (e.g., Vogelsang 1998; Wadley 2015; Goncalves et al. 2016), with the exception of Botswana (e.g., Staurset and Coulsen 2014; Robbins et al. 2016). Open-air sites are much more common in the interior, generally with little organic preservation, often poor chronometric control and fewer cultural remains. These factors might play a part in the different archaeological signal from this region (e.g., Wurz 2013). Whereas resolution is much lower during and before MIS 6, the southern African record from MIS 5e onward can be characterized as structured in time and space (Wurz 2013; Wadley 2015). Beginning in MIS 5, the Late Pleistocene archaeology also reveals a marked increase in sites and artefact density associated with higher rates of technological change. Several successive technocomplexes, that are mostly separated in time and sometimes space, have been formulated based on this record (e.g., Lombard et al. 2012).

Reviewing selected behavioral innovations and elements of material culture in MIS 6, the lithic assemblages of this time frame generally do not feature backed pieces, but bifacial technology is known from sites of the Pietersburg technocomplex in northern and interior South Africa (e.g., Sampson 1974; Grün and Beaumont 2001; Beaumont and Vogel 2006). MIS 6 also features patchy evidence for the use of pigment (Marean et al. 2007; Watts 2010; Watts et al. 2016) and the collection of marine shellfish in small amounts at the site of Pinnacle Point 13B (Marean et al. 2007; Marean 2010). The following MIS 5-3 provide a marked rise in complex elements of material culture and behavioral innovations.

In MIS 5, there is increasing evidence for both backed and bifacial lithic technology (Tribolo et al. 2013; Wilkins et al. 2017), including serrated pieces produced by pressure flaking from multiple occupation episodes at Sibudu (>80 ka; Rots et al. 2017). Pigment use becomes a near-ubiquitous behavior found at most sites during the last interglacial (Watts 2002; 2010; Hodgskiss 2012; Dayet et al. 2013; Wurz 2014; Wadley 2015; Kandel et al. 2016) with ochre used as part of paints (~100 ka; Henshilwood et al. 2011) and compound adhesives for hafting stone tools (Rots et al. 2017). Incised patterns on ochre and ostrich eggshell are also found during MIS 5 (Henshilwood et al. 2009; Texier et al. 2013), as are some formal bone tools at Sibudu and Klasies River (d'Errico et al. 2012a; Conard et al. 2014). Long-distance transport of silcrete >200 km is known by geochemical provenancing studies from several sites in Botswana in this timeframe (Nash et al. 2013; 2016). Finally, MIS 5 provides evidence for fresh-water fishing at White Paintings Rockshelter (~94-66 ka; Robbins et al. 2000; 2016) and frequent traces for the systematic exploitation of various marine resources and successful inhabitation of coastal landscapes at over a dozen sizes (Will et al. 2013; Marean 2014; Will et al. 2015; Jerardino 2016).

MIS 4 has attracted most research interest in the last years, as it was thought to be the exclusive timeframe of the Sill Bay and Howiesons Poort (e.g., Jacobs et al. 2008; Henshilwood 2012). Yet, typical elements of the lithic (bifacial points, backed pieces) and non-lithic technology (e.g., abstract engravings; beads) of these technocomplexes can be found before and after, as shown in this review. This being said, MIS 4 still features the highest number of finely made bifacial pieces, sometimes produced by pressure flaking (~77-72 ka) as well as small and standardized backed pieces associated with laminar industries (~65-59 ka; Jacobs et al. 2008; Lombard 2009; Mourre et al. 2010; Henshilwood 2012). MIS 4 provides abundant evidence for import and use of high-quality non-local raw material over longer distances (>50 km)—yet often based on visual provenancing—particularly during the HP (Volman 1981; Singer and Wymer 1982; McCall and Thomas 2012). The frequency of non-lithic material culture reaches a peak during MIS 4 within the SB and HP (Mellars 2006; Mitchell 2008; Jacobs et al. 2008; Henshilwood and Dubreuil 2011). Pigment use continuous to be a common phenomenon, often used in adhesives (Wadley et al. 2004; Lombard 2006; Wadley et al. 2009). The majority of engravings on both ostrich eggshell and ochre of the region derive from MIS 4 contexts (Fig. 2; Henshilwood et al. 2001; Texier et al. 2010; Henshilwood et al. 2014), as do most shell beads (Henshilwood et al. 2004; d'Errico et al. 2005, 2008) and various types of formal bone tools (Henshilwood et al. 2001; Backwell et al. 2008). During MIS 4, people continued to exploit coastal resources and at some sites even intensified and optimized their gathering strategies (Langejans et al. 2012; Will et al. 2015).

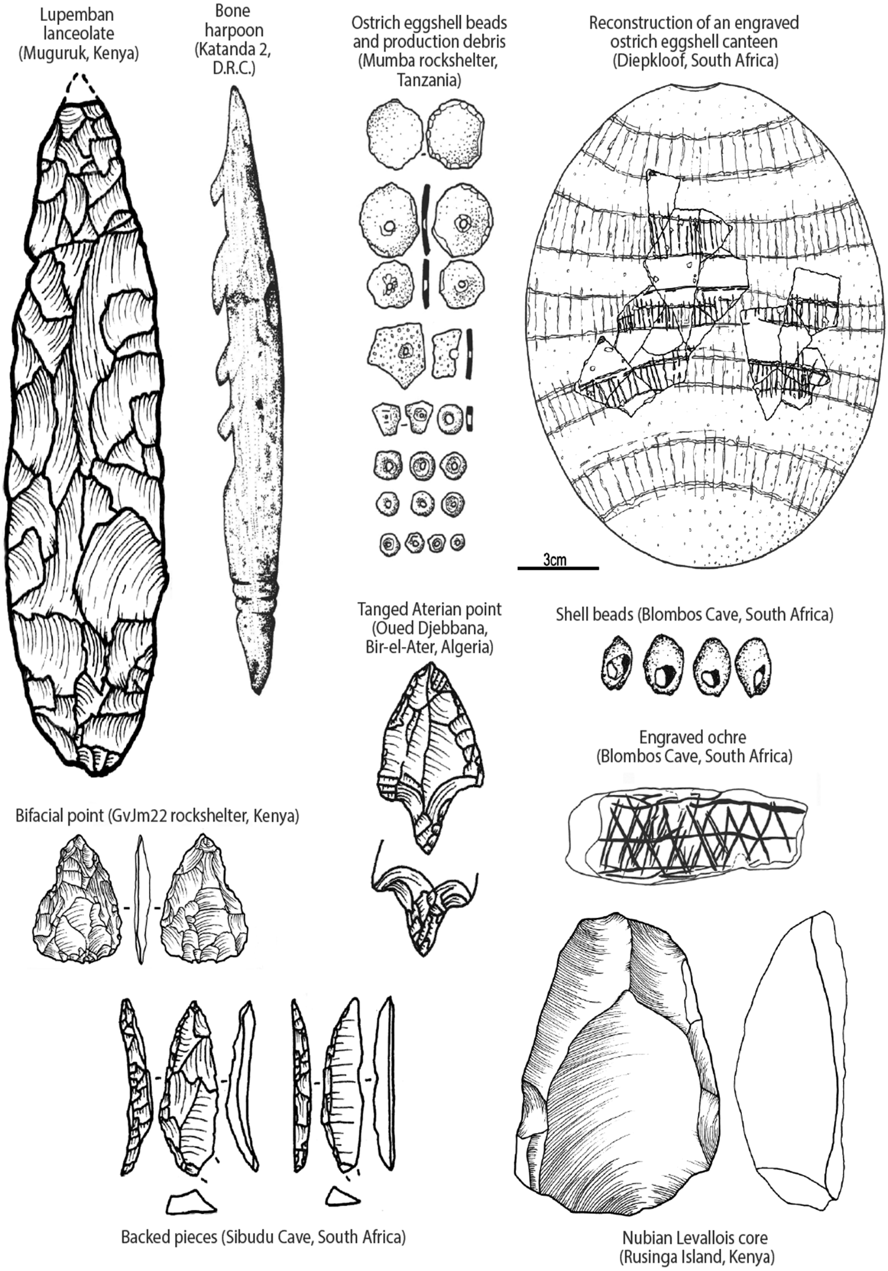


Fig. 2.
Selection of lithic implements and other elements of material culture indicative of complex behavior during ~200-30 ka in Africa. Drawings of artefacts by Sheila Nightingale.

Finally, MIS 3 includes the intermittent manufacture of bifacial points and backed pieces in its early part (~60-50 ka; Steele et al. 2016; Wilkins et al. 2017; Will and Conard 2018) and towards its end, though the latter only in eastern South Africa (~40-30 ka; Wadley 2005; Bader and Will 2017). Both lithic types are found in lower quantities compared to MIS 4. Longer-distance transport of silcrete continues from MIS 4 and lasts until early MIS 3 (~50 ka; Wilkins et al. 2017; Will and Mackay 2017). Ochre sees continued use in high abundance, both as part of compound adhesives (until ~44-42 ka; Lombard 2006; Villa et al. 2012) and of paints (Villa et al. 2015). Rare incised patterns on ochre and ostrich eggshell are known from MIS 3 contexts (Mackay and Welz 2008; Hodgskiss 2013), as are a low numbers of ostrich eggshell, shell and bone beads (d'Errico et al. 2012b; Porraz et al. 2015; Steele et al. 2016). Various types of bone tools occur during early MIS 3 at Sibudu and Klasies River (d'Errico et al. 2012a; Conard et al. 2014) and during mid-MIS 3 at Border Cave (~44-42 ka; d'Errico et al. 2012b). Adaptations to coasts and marine resources continue until early MIS 3, but decrease in their visibility (Will et al. 2014; 2015; Marean 2014).

In sum, the overall pattern emerging from new data deviates from the currently dominant model of a consistent and unilinear trajectory in southern African in which cultural complexity arose and vanished in comparatively short time spans during MIS 4 associated with homogeneous and "precocious" technocomplexes of the HP and SB (e.g., Jacobs et al. 2008; Henshilwood 2012). Recent research and this review find a complex, multi-layered and scale-dependent picture within an overriding trend towards higher complexity during the MSA. During and before MIS 6, there is only constrained and patchy evidence for some of the behavioral innovations and elements of material culture of interest here, which might partially be explained by a low number of documented contexts from this period. The ensuing MIS 5 features the presence and higher frequency of most elements considered here—associated with a higher visibility of archaeological sites—reaches a peak abundance in MIS 4 within the SB and HP, and continues in lower frequency but with the occurrence of nearly all categories until MIS 3 (see also Lombard and Parsons, 2010; Conard et al. 2012; Porraz et al. 2013; Mackay et al. 2014; Kandel et al. 2016). Within this trend, a mix of continuous (e.g., coastal foraging; ochre use) and discontinuous (e.g., shell beads; backing; abstract engravings) indicators of complex material culture characterize the Late Pleistocene record. In addition, some periods (e.g., MIS 5 and MIS 3) evidence multiple regional trajectories in which disparate populations follow divergent pathways as shown in their lithic technology (see Lombard and Parsons 2010; Porraz et al. 2013; Wurz 2013; Mackay et al. 2014; Will et al. 2014).

Northern Africa

The late Middle/Late Pleistocene archaeology of northern Africa (Fig. 1) has a long research history, most closely associated with Francophone scholars since the early 20th century (e.g., Reygasse 1919; Roche 1953; but see McBurney 1960). A spike in interest on this region derives from recent research that has provided rich archaeological sequences in the coastal area and hinterland of the Maghreb associated with a chronometric dating program focused on the Aterian (d'Errico et al. 2009; Dibble et al. 2012; Jacobs et al. 2012; El Hajraoui et al 2012; Douka et al. 2014; Jacobs et al. 2017; Campmas 2018) as well as the earliest fossil finds attributed to *H. sapiens* (Hublin et al. 2017) associated with an early MSA industry dated to ~300 ka (Richter et al. 2017). Geographically, there is a strong research bias on the Maghreb—with much data deriving from deep cave sequences on the coast and hinterland of Morocco and Libya—as well as the Nile Valley (~90% of all dated sites *sensu* Scerri 2017a). With a multitude of surface sites but a low number of stratified archaeological sediments, a lack of organic preservation and few absolute dates in the Sahara and Sahel region, the interior of northern Africa remains comparatively unknown beyond the Nile Valley (Wendorf and Schild 1980; Dibble et al. 2013; Foley et al. 2013; Scerri 2017a). The overall temporal distribution of archaeological sites shows a strong increase in MIS 5 associated with higher find densities, similar to the southern African record. Further resemblances are the occurrence of 'diagnostic' lithic implements (Fig. 2) and evidence for regionalization with multiple named technocomplexes in the region, particularly for the Late Pleistocene (e.g., the Aterian; see for recent discussions Barton and d'Errico 2012; Dibble et al. 2013; Scerri 2013a; 2013b; Campmas 2018). The lack of a supra-regional cultural stratigraphic scheme might be due to a dearth of long sequences as well as a patchwork of dated localities and spatially dispersed sites without chronometric ages (Scerri 2017a).

Lithic assemblages dating to MIS 6 (and before) feature low numbers of bifacial points (Van Peer et al. 2003; Dibble et al. 2013) but no production of small backed pieces. Evidence for the hafting of core-axes is reported from the late Middle Pleistocene at Sai Island (Rots and Van Peer 2006; Rots et al. 2011). Transport of raw material over long distances is virtually unknown or unreported during MIS 6, as are elements of non-lithic material culture of interest here. The site of Sai Island shows the use of yellow and red pigment at the interface of MIS 7/6 (~223-152 ka; Van Peer et al. 2003), but remains a singular case. There is equally isolated evidence for the collection of marine shellfish potentially dating to MIS 6 or even older from Benzú Rockshelter (Ramos et al. 2008; Ramos-Muñoz et al. 2016).

The following Late Pleistocene archaeology of northern Africa (MIS 5-3) encompasses marked changes in stone tool assemblages, with increased geographical structure and more distinct markers in the form of pedunculated tools, small foliate bifacial points and Nubian cores. MIS 5 features a high frequency of sites where tanged tools and small foliate bifacial points are present (Van Peer and Vermeersch 2007; Rots et al. 2011; Barton and d'Errico 2012; Linstädter et al. 2012; Dibble et al. 2013; Scerri 2013a; Scerri 2017a). Some of these pieces were potentially produced by organic hammers (Rots et al. 2011) and pressure flaking (Scerri 2017a). There is an increased use of and more elaborate methods for hafting dating to MIS 5 and onward (Rots et al. 2011; Tomasso and Rots 2017), associated with higher frequencies of tanged, basally thinned and shouldered pieces (e.g., Bouzouggar and Barton, 2012; Scerri 2013b) and potential evidence for the use of resins (Van Peer et al. 2008). From MIS 5 onward there is also good evidence for long-distance transport of raw materials (>20 km and up to 200 km; Van Peer and Vermeersch 2007; Nami and Moser 2010; Scerri 2017a; Campmas 2018) and for the first quarrying of chert in pits (Vermeersch et al. 1997; Vermeersch 2002; Van Peer et al. 2010). Much of the evidence for non-lithic technology in the form of symbolic and organic artefacts in the region dates to MIS 5, frequently associated with Aterian industries. Various types of bone tools in low frequency come from three sites (El Harhoura 2, El Mnasra and Haua Fteah) confined to MIS 5 (Barker et al. 2012; El Hajraoui and Debénath 2012; Stoetzel al. 2014; Campmas 2018). Perforated marine shells used as ornaments are particularly abundant throughout much of MIS 5, deriving from a total of 9 sites with a preference for the use of *Nassarius* shells (dating between ~110->70 ka; Bouzouggar et al. 2007; d'Errico et al. 2009; Nami and Moser 2010; Barton and d'Errico 2012; Dibble et al. 2012; Stoetzel et al. 2014). People frequently transported these shell beads inland with a maximum distance of ~200 km (Vanhaeren et al. 2006). Use of pigment is found at several sites in MIS 5, sometimes on perforated shells, yet without abstract designs (Nami and Moser 2010; Barton and d'Errico 2012; El Hajraoui et al. 2012; Campmas 2018). The Maghreb region has yielded good evidence coastal adaptations during MIS 5 in particular, including the systematic occupation of shorelines as well as planned exploitation of shellfish, with some rare remains of fish, marine mammals and shore birds (Steele and Alvarez-Fernández 2011; Dibble et al. 2012; Steele 2012; Stoetzel et al. 2014; Campmas et al. 2016; Will et al. 2016; Campmas 2018).

The glacial period of MIS 4 is associated with increasing aridity and an overall lower number of archaeological sites. Bifacial technology with pedunculated points and indications for hafting of stone tools are still present (e.g., Rots et al. 2011; Dibble et al. 2013; Tomasso and Rots 2017) and there is some evidence for the earliest production of blades by more volumetric methods and occasional backed pieces within northern Africa (Van Peer and Vermeersch 2007; Van Peer et al. 2010; Garcea 2010; Scerri 2017a). Chert quarrying of raw materials in Egypt as well as occasional long-distance transport of raw materials continues (Vermeersch 2002). Use of colorants and the production of bone tools and shell beads is absent. In MIS 4, there is also a lower number of sites from the coast perhaps due to shoreline flux, but their presence indicates enduring exploitation of various marine resources (e.g., Will et al. 2016; Campmas 2018). The archaeology of MIS 3 features production of bifacial and tanged technology until its early part (e.g., Dibble et al. 2013), sometimes in association with elaborate hafting methods (Rots et al. 2011) as well as increasing production of blades with volumetric methods and small backed pieces at some sites (Van Peer and Vermeersch 2007; Van Peer et al. 2010). Frequent small backed pieces, however, only appear in the Upper Palaeolithic and Epipalaeolithic of MIS 2 (Bouzouggar et al. 2008; Linstädter et al. 2012). An intensification of chert quarrying activities is found for MIS 3 contexts (Vermeersch 2002; Van Peer et al. 2010). Elements of non-lithic material culture considered here have not been reported for MIS 3. Coastal adaptations peter out in early MIS 3, known from only a handful of sites in northern Africa (Steele and Alvarez-Fernández 2011; Stoetzel et al. 2014; Campmas et al. 2015).

In sum—and similar to the southern African record—northern Africa shows some evidence for complex behaviors and advanced cognition at the end of the late Middle Pleistocene throughout MIS 7-6 from a few outstanding sites. This is followed by a marked increase at the onset of the Late Pleistocene, associated with more sites and higher find densities particularly in MIS 5. The Late Pleistocene record is characterized by a mix of intermittent traits (e.g., shell beads, bone tools and ochre are mostly or exclusively found in MIS 5) on the background of continuous features (e.g., tanged pieces; hafting of stone tools; coastal foraging), the latter particularly in the realms of stone tool technologies and subsistence adaptations. Many non-lithic and symbolic elements of material culture appear to fade out or are absent in MIS 4, and early MIS 3 in particular, though this could be a result of climatic challenges and fewer known sites. Northern Africa was strongly affected by climatic variation, particularly the extension and contraction of the Sahara: climatic ameliorations within MIS 5 ("Green Sahara"; Drake et al. 2011; Blome et al. 2012) stand out as key periods for the North African occupation records, especially for coastal sites. The potential loss of many innovations in the non-utilitarian realm with the onset of MIS 4 might thus be due to environmental stress, associated with demographic collapses or contractions that led to a disruption of contacts and exchange networks between populations (Wendorf et al. 1993; d'Errico et al. 2009; Garcea 2010; Barton and d'Errico 2012; Linstädter et al. 2012).

Eastern Africa

Within eastern Africa (Fig. 1), relative political stability in Kenya and Tanzania and strong national research traditions have contributed to an extensive and nearly-continuous history of archaeological investigations. As a result, sites from these countries form the majority of the dataset, augmented by field programs in Ethiopia (Kappelman et al. 2014; Sahle et al. 2014; Douze and Delagnes 2016; Brandt et al. 2017; Assefa et al. 2018), and Malawi (Thompson et al. 2018), as well as isolated studies in

Somalia (Gutherz et al. 2014) and Eritrea (Beyin 2013). Little work on sites demonstrably >40 ka in Uganda, Burundi, or Rwanda has been conducted since the 1960s (e.g., Cole 1967a, 1967b; Nenquin 1967), and almost no work at all has been done in South Sudan since that of Philipson (1981). The Rift Valley and associated Great Lakes are the dominant geological features of the region, and most (open-air) sites occur adjacent to them (Tryon and Faith 2013). Notable exceptions include near-coastal limestone caves or shelters in Somalia and in Kenya (Shipton et al. 2018), and rockshelters or inselbergs east of the Rift (e.g., Willoughby 2012; Tryon et al. 2015). The record of securely dated sites is unevenly distributed over time; demonstrating continuity in particular behaviors is difficult until MIS 4 when the number of sites increases substantially. Whereas 'Early' MSA assemblages with $^{40}Ar/^{39}Ar$-dated tephra from MIS 9-7 are well-known (Tryon et al. 2005; Sahle et al. 2014; Blegen 2017; Brooks et al. 2018; Blegen et al. 2018), there are relatively few sites securely dated to MIS 6-5. Exceptions are the Kibish Formation (Shea 2008), Kulkuletti (Douze and Delagnes 2016), and the Kapedo Tuffs (Tryon et al. 2008). Sites from MIS 4-3 are more abundant and distributed over a larger geographic area. Regarding patterns in lithic technology, the MSA from eastern Africa is best described as a mosaic of variation through time and space with variability as key signal (Shea 2008; Tryon and Faith 2013; Lahr and Foley 2016; Blinkhorn and Grove 2018). While research has shown a general decline in average point size over time (Tryon and Faith 2013), there are no formally defined temporally- or regionally-specific variants of points except for tranchet blows on pieces from Gademotta and Kulkuletti during MIS 8-6 variably interpreted as a specific resharpening technique or impact fractures (cf. Douze 2014; Sahle and Braun 2017).

The few dated sites from MIS 6 feature the presence of bifacial points, as do all sites in in eastern Africa from the Middle Pleistocene until the Holocene (Tryon and Faith 2013). Backed pieces do not occur in this time period. Published direct evidence for the hafting of stone tools is rare, restricted primarily to early microwear studies on obsidian artifacts (Wendorf and Schild 1993). The presence of hafting is inferred from studies of stone point size and weight (Brooks et al. 2006; Shea 2006) and impact studies that indicate that at least some stone points were used as projectiles delivered at high velocity as the tip of spears or similar weapons (Sahle et al. 2013). Notably, the impact studies have focused on some of the earliest points from the MSA of eastern Africa from the Gademotta formation (~280-105 ka; see also Wendorf and Schild 1993). Generalizing from this small sample, the evidence suggests that hafted scrapers and points (Ambrose 1998) were adopted already before MIS 6 and might have persisted among groups from hereon. With regard to long-distance transport of raw materials, the diagnostic geochemical signatures of obsidian outcrops (Brown et al. 2013) have facilitated a major program of studying the geographic dispersal of this material. Site-to-source transport distances for obsidian of >150 km are known before and during MIS 6 (Negash et al. 2011; Blegen 2017; Blegen et al. 2018; Brooks et al. 2018). The pattern of the use and movement of obsidian appears to be a persistent one from the late Middle Pleistocene to MIS 2. Although they occur in earlier assemblages (~MIS 9-7; Brooks et al. 2018) ochre and other colorants are absent for MIS 6, as are all other elements of non-lithic technology considered here.

The archaeology of MIS 5 provides a similar picture, with few known sites dated to this time period and a lack of non-lithic material culture. Bifacial points still occur, and rare backed pieces appear within the long sequence at Mumba in MIS 5 (Mehlman 1989; Marks and Conard 2008), though not as a continuous or widespread finds. There is some evidence for long-distance transport of obsidian (~100-80 ka; Negash et al. 2011). Stone tools associated with marine animals are present in nearshore reefs along the Red Sea (e.g., Sahle and Beyin 2017), with finds at Abdur interpreted as human use of marine resources, but so far limited to MIS 5e (Walter et al. 2000). Evidence for coastal foraging is overall sparse, in part because of the rarity of excavated sites with deposits >40 ka along (or near) the Indian Ocean coast. Fish fossils at sites at Aduma in the middle and later part of MIS 5 (~100-80 ka; Yellen et al. 2005) and perhaps along the Blue Nile (Kappelman et al. 2014) suggest predation of fish along inland river systems during the same time. Evidence for intensive use of aquatic resources around the major lakes is lacking, although the geological record may be partially responsible for this lacuna (e.g., Tryon et al. 2016).

During MIS 4, the number of dated sites increases markedly. Lithic assemblages still feature bifacial points and mostly lack backed pieces (but see Leplongeon et al. 2018). Obsidian from sources in central Kenya were intensively used, and by MIS 4 small amounts of artifacts from these sources occur at sites >300 km distant (Merrick and Brown 1984; Merrick et al. 1994), with similar transport distances found for localities in Ethiopia (Negash and Shackley 2006; Negash et al. 2011). The mechanisms responsible for the movement of obsidian remain unclear (e.g., exchange, embedded procurement, or direct procurement to quarries). By MIS 4 (and MIS 3), evidence for processing ochre is present at nearly every intensively occupied rockshelter in the region, including Porc Epic, Kisese II, Mumba, Panga ya Saidi, Enkapune ya Muto, as well as Chaminade (Ambrose 1998; Conard 2010b; Thompson et al. 2012; Rosso et al. 2016; Shipton et al. 2018; Tryon et al. 2018). The earliest and single case for the manufacture of marine shell beads (*Conus* sp.) has recently been reported from Panga ya Saidi during MIS 4 (~67-63 ka; Shipton et al. 2018). This indicates a pattern of bead use comparable to southern and northern Africa, with marine shell beads preceding the manufacture of ones made of ostrich eggshell. Foraging of coastal or freshwater resources is lacking form the record of MIS 4. During the following MIS 3, backed pieces (Fig. 2) appear at multiple sites in high frequency for the first time (at ~50-40 ka; e.g., Ambrose 1998; Gliganic et al. 2012; Shipton et al. 2018; Tryon et al. 2018). At several of these rockshelters, backed pieces persist after their initial introduction well into the Holocene (Mehlman 1989; Leplongeon 2014; Leplongeon et al. 2018; Tryon et al. 2018). The long-distance transport of obsidian resumes in this timeframe (e.g., Merrick and Brown 1984; Merrick et al. 1994). Moreover, the archaeology of MIS 3 sees a marked increase and diversification in non-lithic material culture. Ostrich eggshell beads (Fig. 2) occur among a number of assemblages at or near the 'MSA/LSA transition' (~50-40 ka; Miller and Willoughby 2014; Tryon et al. 2018), and naturally perforated shells of terrestrial gastropods were potentially used in a similar way in late MIS 3 (~43-33 ka; Assefa et al. 2008). Clearly modified bone tools are restricted to two notched bones from Panga ya Saidi from MSA/LSA levels dated to the middle and end of MIS 3 (~48-25 ka; Shipton et al. 2018). Ochre use is still frequently present in most rockshelter sites of the region, but without abstract designs. Yet, linear engravings on ostrich eggshell fragment were recently found for the middle and later part of MIS 3 at Goda Buticha (~43-34 ka; Assefa et al. 2018).

In summary, elements of complex material culture and other behavioral innovations appear in the late Middle Pleistocene associated with the earliest MSA sites in the region (e.g., Brooks et al. 2018). Eastern Africa shows long-term stability in the manufacture of bifacial pieces, long-distance transport of raw materials and potentially hafting. There is, however, a noticeable gap of non-lithic artifacts and a dearth of sites in MIS 5—contrasting with southern and northern Africa—with many elements of complex material culture (e.g., beads; bone tools; backed pieces) occurring only in MIS 3 in eastern Africa (at ~50-40 ka, near the early MSA/LSA transition). Once these elements appear in the record they generally persist throughout to the LSA, with the exception of a bimodal pattern of backed pieces at Panga ya Saidi (Shipton et al. 2018). These general trends are underlain by a mosaic in lithic technology with a key signal of variability, little spatio-temporal patterning and a dearth of 'diagnostic' artifacts. The overall differences of this record to the Late Pleistocene archaeology to the north and south might have some roots in the abundance of open-air sites and frequent lack of organic preservation, but also in a different ecology. Eastern Africa has a much more variable and patchy ecology with low seasonality as well as high relief and habitat heterogeneity (i.e., volcanism, Rift Valley). Some of the differing cultural patterns observed might be due to more localized adaptations, isolation and extinctions or small population size/density (Basell 2008; Tryon and Faith 2013; Lahr and Foley 2016).

Central and western Africa

In contrast to southern, northern and eastern Africa, the central and western parts of the continent around the Equator (Fig. 1) have received far less scholarly attention and remain the 'great unknown'. Although serious research already began by the early 20th century (e.g., Colette 1929;

Wayland 1929; Breuil et al. 1944) the predominant tropical and rainforest environments with acidic sediments, soil erosion, and few sheltered geological structures (i.e., caves) provided severe challenges to discovery of sites and preservation of (organic) archaeological material. Many countries in this region have a long history of political instability and difficult infrastructures with logistical and natural barriers (Taylor 2014; Cornelissen 2016; Taylor 2016; Scerri 2017b). The known MSA record consists of many open-air sites, many of which have been altered post-depositionally by biogenic processes leading to large-scale disturbances that produce low stratigraphic and cultural integrity (Cahen and Moyerson 1977; Allsworth-Jones 1987; Cornelissen 2002; Mercader 2002; Casey 2002; Taylor 2011; 2014; Chevrier et al. 2018). It thus comes of little surprise that there are few dated sites and few ages beyond 40 ka. This being said, important work has been carried out on the margins of central Africa (e.g., Twin Rivers, Kalambo Falls; Clark 1963, 2001; Barham 2000, 2002a; Barham et al. 2015) and the Semliki Valley (Yellen et al. 1995). In Western Africa, Senegal and Mali have received renewed attention and field work associated with chronometric dating programs (e.g., Chevrier et al. 2016; Scerri et al. 2017; Chevrier et al. 2018).

Due to the rarity of well-stratified and securely dated sites, there is almost no evidence for the spatio-temporal structure of the late Middle-Late Pleistocene record. The age and relationship of the primary archaeological entities in central Africa, the Sangoan, Lupemban, and Tshitolian, remain debated (e.g., McBrearty 1988, 1992; Clark 2001; Barham 2000, 2002a; Taylor 2011, 2016; Cornelissen 2016). In Western Africa, the sequence does not feature a Lupemban (e.g., Casey 2002; Taylor 2016; Scerri 2017b; Chevrier et al. 2018) but a long duration of the MSA from the end of the Middle Pleistocene all the way until the Terminal Pleistocene/Holocene boundary (MIS 2/1), persisting alongside equally aged LSA assemblages (e.g., in Senegal until ~12 ka; Chevrier et al. 2016; Scerri et al. 2017). Well-studied sites in western Africa (i.e., Senegal) yield a temporal signal of high variability regarding both core reduction and tool assemblages with rapid rates of change, and a local mosaic lacking long-term continuity (Robert et al. 2003; Scerri 2017b; Chevrier et al. 2018).

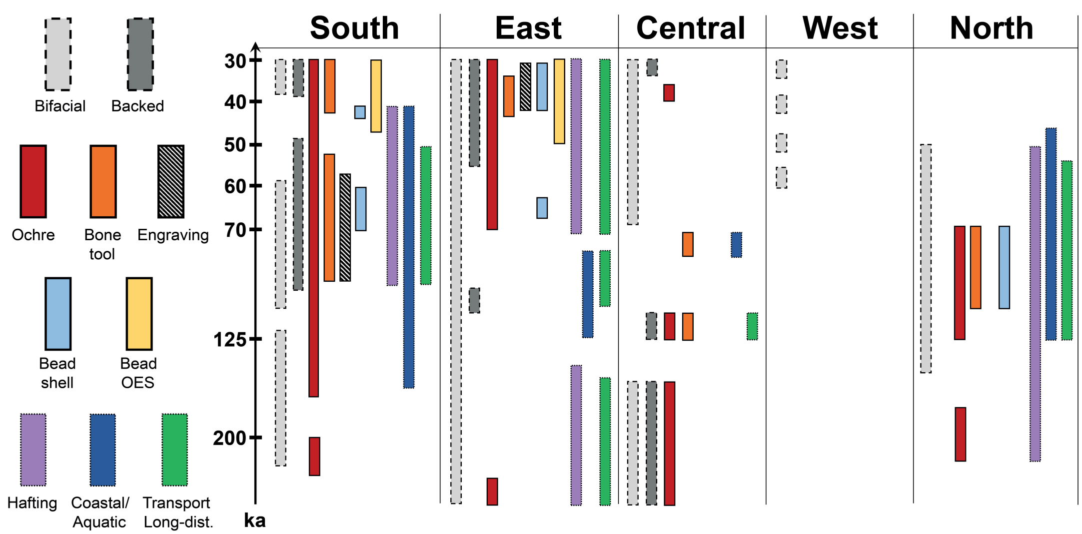
Difficulties in chronometric dating severely hamper the ability to pinpoint evidence for complexity in lithic technology >40 ka. The archaeology of MIS 6 and before features both bifacial shaping of finely-made large lanceolate points (Fig. 2) and the manufacture of small backed pieces in central Africa within a Lupemban context (earliest ages ~270-170 ka at Twin Rivers and Kalambo Falls; e.g., Barham 2000; Clark 2001; Barham 2002a), but not in western Africa. Similar-aged and well-published evidence for the use of ochre comes from the central African sites of Twin Rivers for the use of specularite (Barham 2000, 2002b; Watts 2009) and the later Lupemban at Kalambo Falls (Clark 2001). Concerning hafting, such Lupemban tools are suitable for attachment to handles as part of weapons or heavy-duty axes (Clark 1959; Barham 2001; 2002a; Taylor 2011; 2016), yet direct evidence from lithic use-wear analyses has come only from similar implements in northeastern Africa (Rots et al. 2011; also Taylor 2011; 2014). There is no data available on long-distance transport of raw materials in MIS 6 in central or western Africa, nor finds of other elements of non-lithic material culture.

The following interglacial has yielded backed tools during MIS 5e at Mumbwa Caves (Barham 2000), but there is no evidence for standardization or preference of non-local raw materials for these pieces (Barham 2002a). Potentially due to a dearth of sites dated to MIS 5, no bifacial technology is known in this timeframe in central or western Africa. Long-distance transport of stone tools is rare but documented at sites near the margins of these regions, at Mumbwa Caves up to 200 km during MIS 5e (Barham 1995, 2000) and from undated Aterian levels at Adrar Bous, Niger (Clark et al. 2008). Large blocks of haematite with anthropogenic traces during MIS 5 come from the single site of Mumbwa Caves in central Africa (Barham 1995, 2000). A unique and exceptional find for this region during late MIS 5 are the carefully worked barbed bone harpoons from Katanda (~80-70 ka; Yellen et al 1995; Feathers and Migliorini 2001). The only other potential bone tools in this timeframe is are a single fragment of a pointed polished bone each at Mumbwa (MIS 5e; Barham 1995, 2000) and Broken Hill (Kabwe; Barham et al., 2002). There is also evidence for freshwater fishing from Katanda in MIS 5a, and riverine adaptations continue at other sites of the region until the LSA (Brooks et al. 1995; Yellen 1998). Evidence for adaptations to coastlines are nearly unknown for MIS 5-3 in central and western Africa, likely associated with issues of preservation and little research along coastlines (though occupations in the coastal ecozone of West Africa are known in mid-MIS 3 at ~44 ka; Niang et al. 2018). Due to unfavorable faunal preservation and lacking control on the anthropogenic origin of zooarchaeological material (e.g., Taylor 2014; Chevrier et al. 2018), little else is known about hunting strategies during the Late Pleistocene of western and central Africa.

During MIS 4, there is again some evidence for the presence of bifacial lanceolate points in central Africa. Other types of bifacial foliate points are known from western Africa, but only in pulses during MIS 4-3 (Scerri 2017b; Chevrier et al. 2018). In western Africa, there is no evidence for backed pieces in the MSA as they only appear during MIS 2 associated with LSA industries (Scerri 2017b; Chevrier et al. 2018). No data on lithic transport distances, the use of ochre or the manufacture of organic artefacts are available for MIS 4. The ensuing MIS 3 features the late persistence of lanceolate points potentially indicating long-term stability in this technology, and the carefully shaped tanged bifacial points of the 'Tshitolian' may also date to this interval (e.g., Cornelissen 2002). Small backed pieces appear again in central Africa toward the very end of MIS 3. Non-lithic cultural remains are sparse to non-existent during this time period in central and western Africa. The only available evidence derives from large blocks of haematite with anthropogenic traces from Mumbwa during the middle of MIS 3 (~40 ka; Barham 1995, 2000).

Summary statements on patterns of behavioral complexity in central and western Africa are severely hampered by the low spatio-temporal resolution of the record, requiring more intact and datable stratigraphic sequences favorable to organic preservation (e.g., Taylor 2011, 2016; Scerri 2017b). The available evidence from central Africa points to long-term stability and continuity in technology from (before) MIS 6 until MIS 3, without demonstrated responses to variable climates (Barham 2000; Mercader 2002; Taylor 2011, 2016). This region features early evidence for the use of pigments, sophisticated lithic technologies (e.g., backed pieces; bifacial points) and adaptations to rainforest environments already in MIS 8-6. Some of these elements persist or appear until early MIS 5—or even until late MIS 5 as is the case for the exceptional barbed points from Katanda—though not in MIS 4-3. Non-lithic material culture is virtually absent for 200-30 ka in western Africa, with little information on subsistence patterns or organic remains. In contrast to central Africa, however, lithic technology shows much more temporal variability and higher rates of change with many discontinuous elements of lithic technology during the Late Pleistocene (e.g., bifacial pieces) particularly in the Sahel, a potential response to repeated short-term latitudinal shifts in local habitats in this area. There is also a late persistence of MSA technology until the beginning of the Holocene and evidence for spatial differences in lithic technology between arid and more forested regions (e.g., Scerri 2017b; Chevrier et al. 2018). This being said, these diverging patterns could result from research bias, poor organic preservation and the few stratified sites in either region. Central and western

Fig. 3. Summary diagram for the appearance and timing of different elements of complex material culture and behavioral innovations during the MSA by the different regions. Note the divergent trajectories between different parts of the African continent.



Africa still hold a vast untapped potential, yet have so-far only yielded glimpses of advanced behaviors and complex material culture within a coarse-grained archaeological record.

DISCUSSION AND CONCLUSIONS

The pattern and timing of cultural change during ~200-30 ka in Africa

We reviewed selected aspects of lithic technology, non-lithic material culture and behavioral innovations in southern, northern, eastern, central and western Africa, focusing on spatial and temporal trajectories: when, where and for how long did certain innovations and complex behaviors occur during ~200-30 ka? Our results reveal a main pattern of different trajectories in cultural change among African regions, with the presence, abundance, timing and duration of many innovations not well-synchronized across the various parts (Fig. 3). Our review thus fails to reject the null hypothesis that each region has its own archaeological pattern. In other words, there is no pan-African trajectory for the cultural evolution of *Homo sapiens*.

Looking at these patterns in more detail, the temporal distribution of more frequent shell beads in northern Africa (MIS 5) contrasts against peak frequencies of similar items in southern Africa in MIS 4 and ostrich eggshell beads even later in MIS 3 in eastern Africa, whereas no beads are found in the rest of the continent from 200 to 30 ka. Bone tools appear sporadically and early in central and northern Africa, more frequent and enduring in southern Africa, yet appear only very late in eastern Africa. People used ochre in most regions by MIS 6 and before, but evidence for such pigments is lacking during MIS 4-3 of western and northern Africa, when it is still abundantly present in the southern and eastern areas. Regionalization in lithic technology, such as specific variants of bifacial points and backed pieces, likewise varies in first appearance and temporal trajectory (late vs. early; intermittent vs. permanent). Whereas coastal adaptations are widespread in northern and southern Africa during MIS 5-3, they are (almost) unknown at the coasts of eastern and western Africa.

Rather than a gradual accumulation of complex material culture, the regions show a mix of continuous and discontinuous traits (northern and southern Africa) and a mosaic of technologies with many stable components (western, central and eastern Africa; Fig. 3). Enduring behaviors are particularly found in lithic technology and subsistence whereas non-lithic material culture is more variable, which could in part be due to differential preservation. A marked increase in sites and find density for MIS 5 in northern, southern and western Africa does not occur in central and eastern Africa—with both having stronger Middle Pleistocene signatures (and for the later MSA in eastern Africa). These observations match Lahr and Foley's (2016: 224) conclusion that "the most striking observation of the MIS 5-4 period is the marked contrast between East, South and North Africa."

Many of the large geographical areas we surveyed attest to intra-regional spatial structure that is rarely acknowledged in large-scale overviews: examples are marked differences in the record between coastal and interior southern Africa (Wurz 2013), arid vs. more forested regions of West and Central Africa (Scerri 2017b), the Maghreb vs. the Nile Valley (Scerri 2017a), the age of late MSA assemblages in Ethiopia vs. Kenya (Tryon et al. 2018) or the mosaic of lithic technologies in western Africa (Chevrier et al. 2018). The most detailed studies combining both space and time can be found for the high-resolution record of southern Africa. Here, MIS 3 and potentially MIS 5 yield multiple localized cultural trajectories with different demographic histories, emphasizing the importance of scale in studies tracking cultural change on the level of tens of thousands of years (e.g., Porraz et al. 2013; Mackay et al. 2014; Will et al. 2014).

There are also a few parallels that underlie the different cultural trajectories, at least in some parts of Africa. Such findings are particularly interesting as they run counter to the null hypothesis adopted here. Evidence for complex material culture is present at MIS 6—mostly in low frequency—in all regions and, expect for central Africa, shows a marked increase with the beginning of MIS 5 (northern and southern Africa) and an overall higher frequency and variability in material culture closer to 40 ka (southern and eastern Africa). Similar ages for the earliest occurrences of many innovations in material culture and subsistence in the African MSA have already been noted by Scerri (2017a), and central Africa can be added to this list for ochre use and potentially hafting. For most regions—barring central/western Africa where data are lacking—long-distance movement of materials is well-known for the late Middle and Late Pleistocene. Except for central Africa where the chronology is particularly insecure, one can argue for an overall increase in variability and complexity of lithic technology from the late Middle Pleistocene and throughout the Late Pleistocene as done so previously by Perreault et al. (2013), though there is neither a linear increase in any region, nor do uniform patterns emerge between regions during MIS 5-3 (e.g., in bifacial technology).

Based on our null hypothesis, the similarities between the better-resolved northern and southern coastal records require explanation. These similarities—as well as differences of each to eastern Africa—appear to be the result of behavioral adaptations to comparable environments and commensurable demographic factors (e.g., Tryon and Faith 2013; Lahr and Foley 2016). This might also be a function of known sites with radiometric dates, requiring further testing for such sample bias (see discussion in Blome et al. 2012). Notwithstanding these challenges, this review highlights the spatial and temporal complexity of cultural change during 200-30 ka and within the MSA. Some parallels on large scales exist between regions such as northern and southern Africa (see e.g., Scerri 2017a), with such convergences likely triggered by comparable stimuli that generated similar solutions, but a signal of multifaceted differences on smaller scales dominates the overall picture (Fig. 3). These results underscore the necessity for spatially explicit models regarding the cultural evolution of *H. sapiens* on the vast continent of Africa.

As limitations to our findings, we again emphasize issues of comparability between regions and the scale of analysis. It is important to distinguish between non-behavioral and behavioral factors for the observed differences between regions: Are divergent patterns due to different geologies, geographies, conditions of preservation, chronological problems and research histories—ultimately a result of the nature of the archaeological record—or do they reflect real differences based on varying adaptive strategies to changing environments or distinct demographic and cultural histories? While answering these questions is beyond the scope of this contribution, some observations can be made here. Central and western Africa are most heavily affected by non-behavioral factors and current data need to be considered as providing only a glimpse of the full record. Some of the observed temporal discontinuities in all region might equally be the result of incomplete archaeological sampling and discovery bias, masking a continuous past reality. Interestingly, however, we did not observe a simple taphonomic fall-off curve of non-lithic material culture in most regions for MIS 6-3. That is, the abundance of non-lithic material culture does not appear to be exclusively related to site age in our sample, hinting at the presence of differing adaptive, demographic and cultural factors at work.

Implications for models of cultural evolution in *Homo sapiens*

How do the observed patterns on behavioral innovations and complex material culture in the African record match with empirical expectations deriving from the various models of cultural evolution in *H. sapiens* (Table 2)? At the scale of the African continent, there is now ample evidence from the archaeological record of southern, eastern, northern and central Africa for rejecting Klein's (1994, 2000, 2008, 2009) model of a sudden origin of behavioral modernity within Africa at a late point around ~50–40 ka (see also McBrearty and Brooks 2000; Henshilwood and Marean 2003; Lombard 2012; Conard 2013). Moreover, recent studies found neither neurological nor genetic bases for a revolutionary change taking place during MIS 3 (Mallick et al. 2016; Neubauer et al. 2018). Many behavioral innovations, such as the manufacture of shell beads, bone tools, and abstract engravings can be traced back to MIS 5 throughout various regions of Africa. Other behaviors such as ochre use, hafting and coastal foraging even date to MIS 6 or earlier. These observations are more in agreement with the early and gradual accretion model by McBrearty and Brooks (2000) and scenarios that emphasize the role of coastal adaptations in eliciting an early onset of cultural complexity (Parkington 2001, 2003, 2010; Marean 2015, 2016) drawing upon nutri-

	Late MP complexity	Complexity prior LSA	Regional trajectories?	Unilinear/ cumulative cultural change?	Causality specified?
Gradual and cumulative	X	X	-	X	-
Sudden origin LSA	-	-	-	-	X
Coastal complexity 1 / 2	- / X	X / X	- / -	X / -	X / X
'Synthetic Model'	-	X	n.a.	-	X
Mosaic Polycentric Modernity	X	X	X	-	-
Review empirical evidence	**X**	**X**	**X**	**-**	**n.a.**

Table 2.
Comparison of empirical evidence of this review with expectations from different cultural evolutionary models of modern humans in the MSA.

tional and biochemical studies (e.g., Broadhurst et al. 2000; Kyriacou et al. 2014). Yet, the evidence for coastal foraging is weak in western and eastern Africa, populations from non-coastal regions have also produced early evidence for advanced material culture and Neanderthals show broadly comparable behaviors (see Will et al. 2019, for a detailed discussion). More empirical and theoretical research is required to clarify the specific role of coastal adaptations for the cultural evolution of *H. sapiens*.

Our review 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), even though we did find some long-term background signals of increasing complexity in most regions. Whereas McBrearty and Brooks (2000: 456) initially formulate the expectation that a gradual process need not imply a unidirectional trajectory that unfolds similarly in each region—comparable to the null hypothesis assumed here—they do not take an explicit spatial approach in the presentation of their results or the discussion of their findings. The apparently divergent findings between our study and McBrearty and Brooks (2000) can thus partially be explained by the use of different analytical units, the latter using Africa as a single entity versus individual regions of the continent as employed here. In addition, much better chronological control (due to advances in dating methods other than ^{14}C) of the markedly increasing empirical data throughout the last 15 years, particularly concerning non-lithic material culture, has furthered the understanding of temporal trajectories in different parts of the African continent. Considering this mounting material evidence from Africa, the period 200-30 ka can best be characterized by multiple, temporally variable and non-linear trajectories in different regions such as southern (Conard 2008; Lombard 2012; Conard et al. 2014; Mackay et al. 2014; Wadley

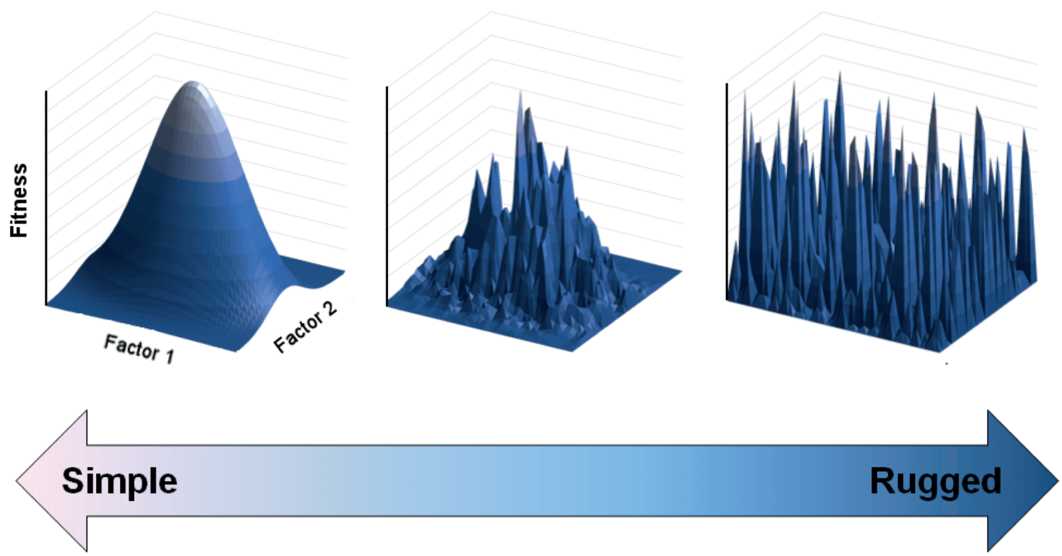
2015), eastern (Tryon and Faith 2013; Lahr and Foley 2016), northern (Van Peer and Vermeersch 2007; Dibble et al. 2013; Scerri et al. 2014), central and western Africa (Taylor 2014; Scerri 2017; Chevrier et al. 2018). Regarding the expectations derived from the geographically more constrained Synthetic Model (Table 2), we find little evidence for a unilinear and discontinuous pattern of cultural evolution in the MSA of southern Africa with a unique peak of behavioral complexity in MIS 4 (Jacobs et al. 2008; Henshilwood 2012). Instead, southern (and northern) Africa is characterized by a mix of continuous and discontinuous elements of cultural complexity and multiple regional pathways throughout most of the Late Pleistocene.

Returning to the continental scale and the last model, the empirical pattern of cultural change by geographic regions in the African record presented above match best with Conard's (2005, 2008, 2010, 2013) idea of "Mosaic Polycentric Modernity" (Table 2). This model rejects a single-origin and unilinear trajectory of cultural evolution in favor of an explicit viewpoint of spatiotemporally variable and intricate historical developments contingent on multiple factors, assuming the presence of equal behavioral and cognitive capacities across regionally separated hominin populations during 200-30 ka. Strictly speaking, this approach would suggest that using 'Africa' as a bounding unit of analysis may also represent a poor fit; the Levant may be a better comparison for northern Africa than areas south of the Sahara. Elements of this model fit with recent theoretical developments which tend to repudiate gradual, linear and cumulative scenarios of cultural evolution for early modern humans. Such concepts instead favor non-directional patterns of cultural change with a focus on historical contingency, cultural capacities, behavioural flexibility, environmental context and path-dependency (e.g., Kuhn 2006; d'Errico and Stringer 2011; Barton and d'Errico 2012; Lombard 2012; d'Errico and Banks 2013; Wadley 2013; Haidle et al. 2015; Kandel et al. 2016; Lahr and Foley 2016; Wynn et al. 2016).

Conard's descriptive model matches the increasingly complicated Stone Age archaeological record of the different African regions in space and time. But how can we best explain the formation of such patterns? To expand the model from an analytical point of view, we draw upon recent theoretical ideas of rugged cultural and fitness landscapes (Kuhn 2006; Lombard 2012; 2016; see also Kandel et al. 2016). Viewing behavioral, cultural and cognitive performances from the perspective of complex, multi-dimensional fitness landscapes draws an analogy to 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 (Fig. 4). Recently, archaeologists such as Kuhn (2006) and Lombard (2012, 2016) have adopted this concept for socio-cultural systems with peaks of different height standing for higher fitness or cultural complexity, reflecting the influence of multiple factors. One can apply such analogies to the African record during 200-30 ka: adding separate regions with different geological, geographical, environmental, biological and demographic factors to a 'global' fitness landscape will create complex spatial topographies. One can predict that these conditions will rarely result in single, optimal and stable pan-African solutions or adaptations. Rather, early modern humans were confronted with a multitude of local, sub-optimal fitness states varying dynamically by region, with change over time in an often asynchronous manner over the continent due to different external or internal stimuli. Rarer periods during which external and internal factors acted in a similar way on different regions might result in broadly comparable solutions (e.g., northern vs. southern Africa during MIS 5). In addition, information transmission between connected groups can serve as attractors to reach similar adaptive peaks, creating regionally homogenous signals during certain circumstances, but also leading to further divergence between regions based on the assumption of population sub-structure on larger spatial scales. Differences in the temporal trajectory between regions can also be amplified by inertia effects, with the differential accumulation of past solutions shaping the paths of subsequent decisions.

The viewpoint formulated here emphasizes that patterns of cultural evolution are spatially susceptible, affected by multiple factors and historically contingent on the initial conditions of populations (path-dependency). These ideas share common ground with mathematical models that emphasize a link between time, demography and cultural complexity (e.g., Shennan 2001; Henrich 2004; Powell et al. 2009; Kolodny et al. 2015) and the ideas of complex systems in which the interconnectivity and number of agents ("NK landscapes") plays a crucial role in governing cultural complexity and change (Kauffman 2000; Bentley and Maschner 2003). We thus argue for an approach of complex landscapes of cultural evolution for the early behavioral trajectory of *H. sapiens*.

Fig. 4.
Idealized model for the theoretical concept of a fitness landscape, simplified to three dimensions. Simpler landscapes feature only one or a few evenly distributed peaks, whereas more rugged landscapes have several peaks of different heights with intersecting valleys (modified after Thomas Shafee; CC BY-SA 3.0).



Future directions: Comparative studies, population substructure and causal mechanisms

This last section outlines some of the key directions where we think that future research should proceed. From a general perspective, assessing the timing and trajectory of behavioral change and cultural evolution in the African archaeological record requires more empirical data from fieldwork in understudied regions but also new methodological strategies and theoretical approaches. Further evaluation of models for the cultural evolution of *H. sapiens* in Africa could be built on explicit inter-regional comparisons that take research and preservation bias as well as temporal variability into account. An essential point will be the analyses of combined archaeological and chronometric data by more quantitative analyses based on statistical and modelling approaches. Crucially, such work can only be undertaken when the current situation with a multitude of local and regional approaches, methods, definitions and nomenclatures, is transcended, requiring a common baseline and analytical grammar for research, particularly in the study of stone tools. Two of us (CT and MW) have initiated such a process with the CoMSAfrica network ("Comparative analyses of Middle Stone Age artefacts in Africa") which brought together researchers working in different areas of the continent together in a workshop at the end of 2018 to discuss such ideas (Will et al. n.d.).

Comparative approaches will also be necessary to evaluate propositions of marked population substructure of early *H. sapiens* taken from genetics and biological anthropology (Gunz et al. 2009; Harvati et al. 2011; Lahr 2016; Mallick et al. 2016; Schlebusch et al. 2017; Skoglund et al. 2017) from an archaeological point of view. Some promising archaeological work on smaller local and regional scales has already been undertaken (Scerri et al. 2014, 2017; Blinkhorn and Grove 2018). Yet, only research on larger scales with improved chronologies, including lithic and non-lithic evidence with a common comparative baseline, will allow to further test such concepts. Theoretical ideas of cultural transmission and multidimensional fitness landscapes could provide the necessary bridges between empirical observations and further-reaching interpretations. This approach requires a geographically-explicit perspective and the acknowledgment of a high likelihood of different demographic and behavioral trajectories within the vast African continent.

The causal mechanisms of behavioral change that underlie cultural evolution have been an important point of debate left aside for the most part in this contribution. External environmental causation has a long tradition in archaeological explanation and there is considerable evidence that people during the Paleolithic successfully adapted to climatic and ecological changes. Recent research, however, showed that environmental change must be considered in concert with demographic and sociocultural factors, particularly at finer scales of analyses (Conard and Will

2015; see also Villa et al. 2012; Clark 2013; Porraz et al. 2013; Tryon and Faith 2016). There is also a need to better demonstrate causal links between particular environmental changes and patterns in the archaeological record other than mere correlation (see Chase 2010; Blome et al. 2012; d'Errico and Banks 2013; Marean et al. 2015). Demographic aspects, including population density and interconnectivity, but also the variable pathways of cultural transmission, constitute additional key variables to study and explain complex patterns of cultural change, such as the appearance and disappearance of cultural variants, but also their differential uptake or varying trajectories in separate regions (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Rogers 1995; Henrich 2001; Bentley and Maschner 2003; Henrich 2004; Derex et al. 2013; Kolodny et al. 2015). The spatial heterogeneity seen in the MIS 6-3 record 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. Testing these hypotheses requires better approaches to reconstruct information networks and population sizes during the Pleistocene (see French 2016). Models of cultural evolution should also consider constraints and potentials set by family and social structures, human diet, anatomy and biology (e.g., Rogers 1988; Lieberman 2007; Wells and Stock 2007; Hill et al. 2011; Tattersall 2014; Neubauer et al. 2018), such as the reciprocal impact of changes in genetic makeup and neuroanatomy on cognition and culture (e.g., Laland et al. 2010; Hublin et al. 2015; Wynn et al. 2016; Srinivasan et al. 2018).

From a more theoretical perspective, predominant monocausal explanations neglect the observation that causal factors are not always hierarchic and independent, particularly in complex systems like human culture. Causal mechanisms can further (inter-)act in fundamentally different ways on different scales of time and space (Conard 2001; Bentley and Maschner 2003; Blome et al. 2012; d'Errico and Banks 2013) 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, small initial changes within populations might have had unpredictable, qualitatively different outcomes owing to the complexities and connectedness of human societies, dependent on baseline conditions (Kauffman 2000; Bentley and Maschner 2003).

In conclusion, new models for the behavioral evolution of modern humans should be spatially explicit, and take environmental, biological, demographic, cultural, and social factors into account. These factors interact to form a complex network of causal agents on several scales, consistent with central tenets of gene-culture co-evolution (e.g., Cavalli-Sforza and Feldman 1981; Richerson and Boyd 2005; Laland et al. 2010; Mesoudi 2011), niche construction (Odling-Smee et al. 2003; Laland et al. 2007), and multiple inheritance theory (Jablonka and Lamb 2014). Combining complexity theory with bio-cultural models of evolution, processes of cultural transmission, and complex fitness landscapes could provide a holistic view on the mechanisms and trajectory of cultural evolution of *Homo sapiens* in Africa.

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