
Supplementary information

Major expansion in the human niche preceded out of Africa dispersal

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SI-1 Human Origins: Fossils and Archaeology brief overview

Homo sapiens originated in Africa during the Middle Pleistocene (781-126 thousand years ago or ka). This is supported by fossil, genetic, and archaeological evidence. In Africa, the later part of the Middle Pleistocene corresponds to the archaeological period known as the Middle Stone Age (MSA). The associated fossil record is somewhat sparse. At present the first appearance date of “early or recent anatomically modern” *H. sapiens*¹⁰⁶ is 315 ± 34 ka¹⁰⁷ at Jebel Irhoud, Morocco, in association with MSA technology. The Jebel Irhoud fossils have a modern human facial and dental morphology, but a more archaic braincase morphology¹⁰⁶. Hublin et al.¹⁰⁶ suggest that by about 300 ka, the human facial morphology had been established, while the braincase continued to evolve more recently in *H. sapiens* evolutionary history. The earliest *H. sapiens* fossil that exhibits a modern braincase morphology was recently re-dated to a minimum age of 233 ± 22 ka¹⁰⁸ (previously 155-187 ka¹⁰⁹) and was found in Ethiopia¹¹⁰⁻¹¹². The Omo Kibish 2 fossils include skull fragments and postcranial bones¹¹³⁻¹¹⁵. Similarly robust anatomically modern human fossils dating to ~160 ka were also found at Herto, Middle Awash, Ethiopia¹¹⁶. Anatomically modern human fossils have been directly dated at Qafzeh, Israel to 100 ± 5 ka¹¹⁷. Additional anatomically modern human fragmented cranial and postcranial fossils of a similar age have been recovered at Klasies River in South Africa¹¹⁸. The cranial and mandibular remains from Klasies River fossils include gracile individuals¹¹⁹ as well as robust individuals lacking a pronounced mental eminence¹²⁰. The postcranial remains from Klasies River suggest affinities with both archaic and recent human populations¹²¹. Cranial fragments of anatomically modern human fossils have also been recovered in Ethiopia at Aduma and are dated to ~100 ka¹²². All these fossils consist of a mix of different archaic and modern features¹²³, and it

is not until between 100 and 40 ka that the full constellation of features that defines humans today is found in single individuals¹²⁴.

The archaeological record in Africa underwent a profound shift with the emergence of Middle Stone Age (MSA) technology from around >300 ka. The shift in focus from shaping a block of raw material to removing stone flakes from the block resulted in an explosion of new tool types, not previously seen in the African record, and long thought to be a hallmark of modern cognition¹²⁵. The discovery of very early MSA technology with some of the earliest fossils of *H. sapiens* at Jebel Irhoud has since indicated a link between the biological and behavioral manifestations of MSA humans. Generic MSA technology is not dissimilar to Eurasian Middle Palaeolithic technology in that basic elements include forms of scrapers, retouched points, and denticulates often made using both Levallois and non-Levallois reduction methods. MSA assemblages are generally characterized by featuring a higher frequency and morphological variability of unifacial and bifacial points, as well as basally thinned pieces, which mark them out from Middle Palaeolithic assemblages¹²⁶.

The composition of the MSA flaked stone industries remained largely unchanged until about 130 ka, after which there is remarkable regional and temporal variability. The MSA is followed by Later Stone Age (LSA) technologies, with the earliest evidence of this shift in some regions from around 40 ka¹²⁷, but perhaps as early as 67 ka¹²⁸. The transition between the MSA and LSA over Africa is spatio-temporally complex and not a uniform and parallel process (see Bader et al.¹²⁹). However, relatively brief periods of a marked increase in the frequency of complex material culture and behavioral innovation within the MSA are evident in several regions of Africa, most notably the northern and southern ends of the continent. Many of these innovations do not appear to have had significant continuity and were used to greater and lesser degrees over time that more reflect a complex mosaic rather than a cumulative process³⁴. This notwithstanding, the MSA witnessed a series of key developments, including the emergence of long-distance social networks and the transport of exotic raw material⁴⁸, bow and arrow technology¹³⁰, traps and snares¹³¹, water storage⁷², personal ornaments^{26,27,30,132,133}, geometric engravings^{72,134}, drawings¹³⁵, and stone tool technology that was regionally distinctive both in form^{136,137} and methods of hafting¹³⁸⁻¹⁴⁰.

In southern Africa, a proliferation of traits associated with innovative MSA human behavior appear first between ~100-70 ka. At Blombos Cave, an “ochre processing workshop” was identified from deposits dated to 100 ka³⁷, pierced shell beads were recovered from deposits dated to ~75 ka²⁷, by ~75 ka pressure flaked stone tools are present¹⁴¹, and bone tool technology is present by ~100 ka at Klasies River Main site Cave 1A¹⁴² and occurs more regularly by ~72 ka at Blombos Cave^{143,144} and at Sibudu Cave¹⁴⁵. At Pinnacle Point 5-6, heat treatment of silcrete to improve stone tool manufacture is present by ~72 ka³⁶, microlithic technology is present by ~71 ka³⁵, and dense shell middens¹⁴⁶ are present in sediments dated to 70.6 ± 2.3 ka³⁵. Regionally distinct bone tools have been identified at Sibudu Cave and are from deposits dated to ~72 ka

and ~64-57 ka^{145,147}. Long-term use of diverse marine resources and settlement of coastal landscapes is well-established in southern but also northern Africa between at least ~160-50 ka¹⁴⁸.

In northern Africa, innovative MSA technologies also appear beginning ~100 ka. The collection and use of shells as personal ornaments (eg. *Nassarius* sp. and *Tritia* sp.) appear throughout coastal and inland Morocco ~115 ka³⁰. Pierced *Nassarius* sp. shell beads *in situ* have been identified at Bizmoune and may date to ≥ 142 ka¹³³, at Contrebandiers Cave dated to ~115-96 ka¹⁴⁹⁻¹⁵¹, at El Harhoura 2 dated to ~116-100 ka¹⁵², at El Mnasra dated to 108-106 ka^{41,152}, at Ifri n'Ammar dated to ~83.3 ka^{132,153}, and at Taforalt from deposits dated to ~82.5 ka²⁶. A “bone knife” tool from Dar es-Soltan I cave was identified in Aterian deposits dated to ~90 ka ago¹⁵⁴, and recently available chronologies at El Mnasra estimate the age of bone tool¹⁵⁵⁻¹⁵⁷-bearing Aterian layers to be ~107 ka⁴¹. A worked bone industry was identified at Contrebandiers Cave in deposits dated to 120-90 ka¹⁵⁸.

In northern Africa, the region closest to the land route into Eurasia, cultural changes peaked around the Last Interglacial, the time when early human fossils are also found in the Levant. The basic Middle Palaeolithic (MP) technology in the Levant during this time was not substantially different than the MSA in neighbouring regions of Africa¹⁵⁹. Repeated humid episodes in the Saharo-Arabian arid belt from around 125 ka likely facilitated these dispersals, as well as widespread expansions within the Saharan region itself¹⁶⁰ and now arid areas of the Arabian Peninsula^{161,162}. However, iconic innovations, such as Aterian tanged tools do not appear to cross the Nile¹²⁶. By the beginning of Marine Isotope Stage 4, (MIS 4, 71-57 ka), widespread aridification appears to have driven the contraction or extirpation of many populations in this region¹²⁶. For example, Aterian tanged tool assemblages that had previously dominated vast regions of northern Africa contract to the Mediterranean coast and the central Saharan mountains, where they eventually disappear during this timeframe³². However by the end of MIS 4 and the beginning of MIS 3, multiple, if comparable, trajectories of technological change within the MSA are observed in northeast Africa¹²⁶, perhaps indicating a re-expansion of populations shortly before dispersal out of Africa. At Haua Fteah in Libya, the MSA material culture intermittently continues until about 46-41 ka and is then replaced by a completely different and apparently unique blade-based industry, the so-called ‘Dabban’ around 39 ka⁸⁵. The Dabban post-dates the appearance of Upper Palaeolithic technologies in the Levant¹⁶³, as well as elsewhere in Europe^{164,165}.

By MIS 3, Later Stone Age (LSA) assemblages begin to replace MSA assemblages. The oldest examples of potential LSA technology come from eastern Africa, at Panga Ya Saidi in Kenya, where relevant assemblages have been dated to MIS 4, at around ~67 ka¹²⁸. While the profound economic shift underlying the transition from the MSA to the LSA is not well understood, the lifeways underpinning the LSA spread rapidly throughout MIS 3, until the MSA is all but replaced in most of Africa by ~20 ka^{129,166-168} (but see Scerri et al. (2021)¹⁶⁹). The LSA is usually

denoted by a significant reduction in the size of stone artefacts with a focus on microlithic tools, sometimes appearing in standardized, geometric form, as well as a simplification of lithic technology and an increase in non-lithic technologies^{127,170}. The LSA continued to dominate the African record until the end of the Pleistocene^{171,172}. While LSA populations clearly had different practices than MSA populations and continued expanding into new regions and environments of Africa, they remained hunter-gatherers without evidence for agriculture, animal husbandry or sedentarism, and therefore shared many of the same vulnerabilities with Middle and earlier Late Pleistocene humans. For these reasons, we explore the expansion of the human niche in our study until the end of the Pleistocene.

SI-2 Dispersals within and out of Africa

The oldest MSA sites are found in eastern, southern, and north-eastern Africa⁴². Despite the similarity of the technology, the few associated human fossils are diverse, as discussed above. It seems likely that there wasn't a single, geographically circumscribed 'birthplace' for *H. sapiens*¹, but that various morphs on the *H. sapiens* lineage may have been spread out in Africa. Whether this includes most, or just parts, of Africa is currently not well understood. It is therefore difficult to reconstruct within-Africa dispersals. However, the emergence of geographically discrete and highly distinctive material cultures within the MSA, such as the Aterian and Howiesons Poort technocomplexes, coupled with the diversity of the early *H. sapiens* fossil record, suggests that mixing was not constant.

It has been suggested that some of these early populations may have left Africa relatively early. Genetic studies have suggested that some very early *H. sapiens*, or populations on the lineage leading to us, left Africa and replaced the Neanderthal mitochondrial genome, possibly before 270 kya^{173,174}. Modern looking fossils from Apidima, Greece may also date to >210 ka¹⁵, while fossil evidence at Misliya in Israel is dated to 177-194 ka¹⁴. Later human fossils from Skhul and Qafzeh¹⁷⁵⁻¹⁷⁷ in the Mount Carmel of present-day Israel have yielded dates that suggest a dispersal ~125-82 ka during Marine Isotope Stage 5. A human fossil from northern Arabia was dated to the end of this range, at around 85 ka¹¹.

It is currently very difficult to determine whether these lines of evidence indicate multiple early dispersals, or just one or two¹⁰. Generally, these earlier dispersals are viewed as relating to climatic windows⁸¹ in which Saharo-Arabia greened, thus permitting animals and humans to cross the formerly impenetrable desert barrier into Eurasia. If the dates and taxonomic identifications are correct for Apidima and Misliya, it would seem that dispersal took place during interglacial MIS 7 to early glacial MIS 6. However, the age of fossil remains is not necessarily the age of dispersal, which could have happened much earlier. Whatever the case, these earlier incursions into Eurasia do not seem to have left any genetic legacy in living Eurasian populations. One of the main lines of evidence for this is the Neanderthal ancestry found in all present-day and ancient non-African modern human genomes that have been studied to date. This ancestry is mostly consistent with originating from a single episode of admixture^{2,3,6,7} which had mostly ceased by 50–60 ka^{4,178–180}.

Supplementary Table 1. Database of radiometrically dated Pleistocene occupation layers from archaeological sites in Africa used in this study. This database includes archaeological layers that have published coordinates, radiometric dates, an error range less than or equal to 20,000 years, and a mean age $\leq 120,000$ and $\geq 14,000$ years. Bioclimatic variables for each archaeological layer were accessed from Beyer et al. (2020)⁶² with added Heinrich events.

Supplementary Table 2. Calibration of 14C radiocarbon ages. This database includes the number assigned to each archaeological site name and layer for Extended Data Figure 5, as well as uncalibrated ages and errors, calibrated ages and 1σ errors that were used in the current study, and calibrated ages and 1σ errors that were not used in the current study.

Supplementary Table 3. Tests of spatial autocorrelation in the residuals of the GAM with Moran's I values. This table includes estimates for Moran's I, the expected values and their significance for both fixed-niche and changing-niche models. Each row represents a different resampling of presences and pseudo-absences.

Supplementary Table 4. Biome classifications from Beyer et al (2020)⁶² with added Heinrich events and from PCESM^{63,64}. Translation from the biome categories in the original publications to the three major classes, forest, savannah and desert, as used in our analyses.

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