

Rethinking the Dispersal of *Homo sapiens* out of Africa

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Current fossil, genetic, and archeological data indicate that *Homo sapiens* originated in Africa in the late Middle Pleistocene. By the end of the Late Pleistocene, our species was distributed across every continent except Antarctica, setting the foundations for the subsequent demographic and cultural changes of the Holocene. The intervening processes remain intensely debated and a key theme in hominin evolutionary studies. We review archeological, fossil, environmental, and genetic data to evaluate the current state of knowledge on the dispersal of *Homo sapiens* out of Africa. The emerging picture of the dispersal process suggests dynamic behavioral variability, complex interactions between populations, and an intricate genetic and cultural legacy. This evolutionary and historical complexity challenges simple narratives and suggests that hybrid models and the testing of explicit hypotheses are required to understand the expansion of *Homo sapiens* into Eurasia.

A variety of dispersal models (Table 1) address the period between the widely accepted African origin of *Homo sapiens* by around 200–150 ka and the arrival of our species at the margins of the Old World, including Australia, Siberia, and northwest Europe, by 50–40 ka.^{1–4} The evolutionary, demographic, and cultural processes between these milestones

remain unclear, but a variety of recent studies add important new data.

Whereas earlier models focused on assessing the geographical origins of our species based on fossil data, more recent approaches seek to combine fossil, genetic, archeological, and paleoenvironmental data to illuminate the nuances of dispersal into

Asia (Table 1). These models emphasize different hypotheses concerning factors such as when dispersals began, how many occurred and which routes were followed. Recent models have largely fallen into two broad categories, emphasizing Marine Isotope Stage (MIS) 5 (early onset dispersal model) or post-MIS 5 (late dispersal model) time frames (Table 1). This, however, is not a rigid dichotomy. For example, models proposing an early onset to dispersal are consistent with subsequent post-MIS 5 dispersals having also played an important role in patterns of human diversity.

FOSSIL EVIDENCE

Hominin fossil remains provided the initial foundations for the Out of Africa model.³ Future fossil discoveries in Southern Asia have the potential to radically transform our understanding of that dispersal. Early

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TABLE 1. Summary of Selected Key Models for the Dispersal of *Homo sapiens* out of Their Place of Origin, Presented in Broadly Chronological Order of Formulation^a

Model	Inferred timing of dispersal	Description	Examples of key references
Models focusing on <i>Homo sapiens</i>' origins			
Asian cradle model	Unclear	Asia as birthplace of <i>H. sapiens</i>	5
The SW Asian/NE African cradle model	Unclear	SW Asia and NE Africa as cradle in which <i>H. sapiens</i> evolved and from which it subsequently dispersed	6
Multiregional model	Throughout the Pleistocene	<i>H. sapiens</i> evolved simultaneously in several parts of the world, with species integrity maintained by recurrent gene flow	7
Recent African Origin (RAO) model	~100-40 ka	<i>H. sapiens</i> evolved in Africa, perhaps in one region such as East Africa, and subsequently dispersed	3,4
RAO and hybridization model	~100-40 ka	Accepts RAO, but infers greater levels of hybridization with other hominin species in Eurasia	8-10
Assimilation model	~100-40 ka	<i>H. sapiens</i> evolved in Africa, but subsequent spread represents gene flow rather than replacement	11,12
Variants of Late Dispersal Model			
Multiple dispersals model	MIS 4 (~70 ka) then MIS 3 (~50 ka)	MIS 4 dispersal by southern route to Australia, then MIS 3 dispersal of populations by northern route	13
Upper Paleolithic model	~50-45 ka	Successful out of Africa occurred after 50 ka, with derived technology such as projectiles	14,15
MIS 4 single coastal dispersal model	~75-60 ka	Structure of mtDNA tree interpreted as indicating dispersal around MIS 4	16
Single coastal dispersal with geometric technology model	~60-50 ka	A single dispersal out of Africa followed a coastal route, marked by a trail of geometric technologies and symbolic artifacts	17
Variants of Early Onset Dispersal Model			
Early onset multiple dispersal model	Beginning in MIS 5 (~130-75 ka), also MIS 3 (~55-45 ka) key	Multiple dispersals out of Africa, associated with climatic "windows of opportunity." Early dispersals associated with MP technology	2,18
"Jebel Faya" model	~130 ka	Dispersal out of Africa across southern Arabia with Levallois, blade, and bifacial technologies in MIS 5e	19
"Nubian" model	by ~106 ka	Dispersal out of Africa by MIS 5c marked by presence of "beaked" ("Nubian") Levallois technology in Arabia	20

^aKey references may considerably postdate the initial formulation of particular models.

Homo sapiens was morphologically variable.^{4,21} Traits that characterize *Homo sapiens* include: neurocranial globularity; a divided supraorbital torus and central and lateral portions; the face retreated below the forepart of the brain; a bony chin, even in infants; a gracile tympanic bone; the absence of an iliac pillar; and a short, thickened superior pubic ramus.³ Yet even at a single site, morphological variability can be striking. Omo-Kibish 1, for instance, strongly expresses the derived features of *Homo sapiens*, whereas Omo-Kibish 2, which is believed to be of similar age, is much more archaic.³ Given small samples, it is difficult to tell if the variation of early *Homo sapiens* represents intrapopulation variation or the existence of several highly structured populations by the later Middle Pleistocene. Nevertheless, the fossil record is most parsimoniously interpreted as demonstrating the piecemeal development of *Homo sapiens* in Africa during the later Middle Pleistocene.

The earliest known *Homo sapiens* fossils from outside Africa are found in the Levant, one of the few relatively intensively studied areas in Asia, at the sites of Skhul (~120-90 ka) and Qafzeh (~100-90 ka).³ These fossils display numerous derived traits, with a small number of primitive (archaic) features. Subsequently, *Homo sapiens* are present in the Levant from around 43 or 42 ka,²² and perhaps at around 55 ka (75.2–33.6 ka) at Manot Cave.²³ In the latter case, however, the age estimates come from a calcitic patina or crust that covers the calvaria; hence, these are minimum dates. The specimen may be considerably older and/or may not reflect dispersal from Africa. Stalagmites from the site demonstrate a hiatus in speleothem formation between late MIS 5 and MIS 3. Neanderthal fossils have been discovered in the Levant and elsewhere in Asia dating to ~70-50 ka.^{24,25} Fossil data are consistent with archeological discoveries in suggesting that in the Late Pleistocene, reliably dated Neanderthals are present in the Levant only after MIS 5, when *Homo sapiens*, possibly aside from the Manot Cave cranium, appear to be absent.²¹ This apparently asynchronous timing may

suggest that interbreeding between the species took place elsewhere, that small populations of *Homo sapiens* survived into MIS 4 in the Levant, or that *Homo sapiens* reoccupying the Levant in MIS 3 encountered late Neanderthals.

Vast areas of Asia have yet to produce any Pleistocene hominin fossils.^{26,27} Sites further east face dating problems and taxonomic ambiguities associated with elements such as teeth and foot bones that are not strongly diagnostic of species.^{25,28,29} While the relatively well understood Levantine record may provide a null hypothesis for demographic change across a wider area of Southwest Asia,²⁴ this must be qualified by the

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atypical ecological features of the Levant as a Mediterranean biome in a region more widely characterized by the particularities of the much larger Saharo-Arabian biome.

Dennell has reviewed the fossil record for *Homo sapiens* between Arabia and Australia.²⁵ The oldest South Asian fossils found, from the Sri Lankan cave of Fa Hien, date to ~33-30 ka. In Southeast Asia, the oldest fossils are from the cave of Tam Pa Ling in Laos and date to ~65-45 ka.²⁹ This age admits the possibility that *Homo sapiens* either left Africa earlier than the Upper Paleolithic model suggests or that dispersal was extremely rapid, as hypothesized by coastal dispersal models (Table 1). Several new but preliminary findings suggest that *Homo sapiens* may have arrived in Southeast Asia earlier than was previously thought. The site of Callao Cave in the Philippines has produced a hominin metatarsal dating to ~67 ka,

which is provisionally assigned to *Homo sapiens*.²⁸ Several sites in China are claimed to demonstrate the presence of *Homo sapiens* by MIS 5. However, these sites, which often have poor stratigraphic and chronological control, have produced taxonomically ambiguous specimens.²⁵

GENETIC EVIDENCE

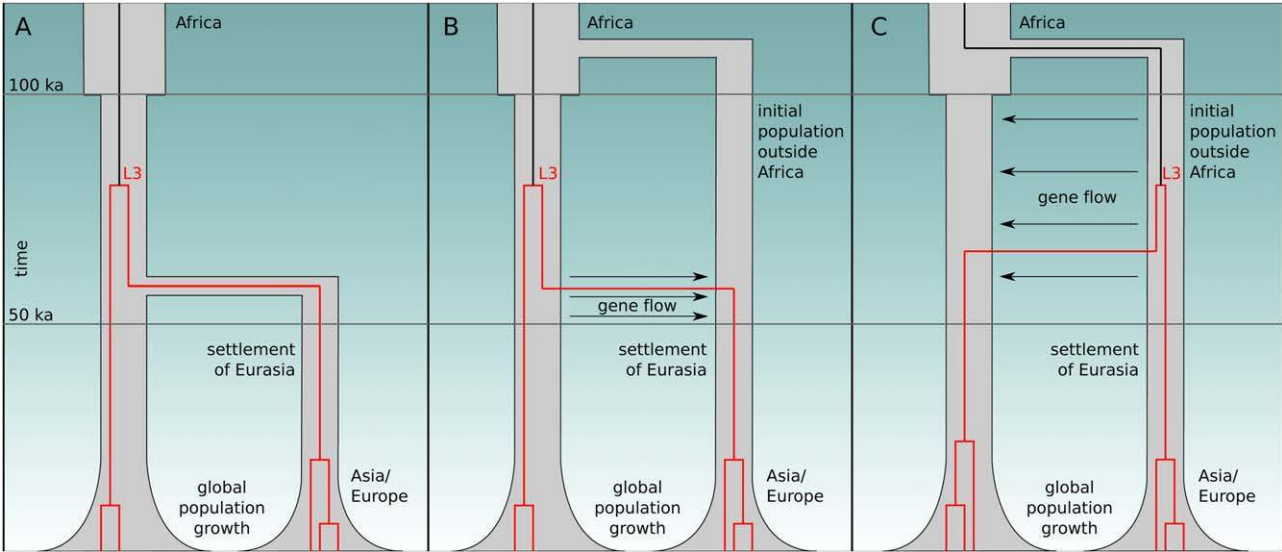
The first reconstructions of human genetic ancestry were based on data from mitochondrial DNA (mtDNA), chromosome Y, and a small number of nuclear loci.^{30–32} Much of what they revealed, such as evidence of a recent African origin of *Homo sapiens*, remains central to our understanding today. However, recent developments have changed the nature of the genetic evidence for human evolution and dramatically increased its scope. New sequencing technologies and computational approaches have enabled large-scale whole-genome analyses of human populations, while the ability to recover ancient DNA sequences from fossils has extended our view of genetic diversity by tens of millennia into the past.

These developments have led to important revisions in how we understand the ancestry of humans and other hominins.³³ For example, it is clear that this ancestry involves a much greater degree of demographic complexity than could previously be resolved, with evidence of pervasive gene flow and admixture between populations.^{9,10,34,35} The relationship between genetic ancestry and demographic history is less straightforward than it was often assumed to be, and requires more sophisticated inferential approaches. Inferences based on the genealogy of a single genetic locus, such as the mtDNA tree, can be problematic, particularly for older events. Such a genealogy represents one random outcome of the genealogical process, the shape of which is only weakly constrained by demography. Moreover, while a simple tree is inadequate to describe the complexity of human ancestral demography, genealogies are always strictly tree-like.

The timing of the dispersal of *Homo sapiens* out of Africa is a case

Box 1. The mtDNA Genealogy and the Chronology of Dispersal out of Africa

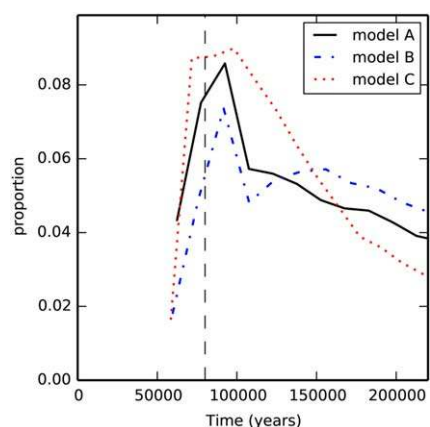
Human mtDNA exhibits a genealogy in which all haplotypes (unique DNA sequences) in present-day non-Africans are placed within a clade or haplogroup, the most recent common ancestor (MRCA) of which has been dated to ~79 to 60 ka.³⁶ This haplogroup, named L3, encompasses several others that are found in modern Africans, predominantly in East Africa.⁹³ This has led to the argument that the MRCA of L3 is an upper boundary on the exit from Africa, and that the mtDNA genealogy is incompatible with an earlier presence outside Africa for the ancestors of present-day humans. This argument, however, rests largely on the assumption that human demographic history has been tree-like (Fig. 1A).¹³ If, instead, we allow for gene flow between the ancestral African and non-African populations after an earlier initial divergence (Fig. 1B, C), then it is possible for L3 to have arisen during this period in one or the other population and still be found in both populations today. Indeed, evidence for ongoing



Box Figure 1. Alternative models of the relationship between the mtDNA genealogy and demographic history. Models B and C illustrate the possibility of an early divergence of African and non-African ancestors to, with subsequent gene flow, potentially congruent with fossil and archeological evidence of a dispersal of *Homo sapiens* out of Africa ca. 100 ka. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

TABLE 2. Demographic parameters and ms commands used for coalescent simulation, Representing exponential growth starting 15 ka in all three populations from an ancestral N_e of 1,500 to a present-day N_e of 25,000 (corresponding to autosomal N_e growth from 6,000 to 100,000, assuming equal male and female N_e); African ancestral N_e of 2,500 100ka; non-African N_e of 500 from 55–40 ka in model A and 80–40 ka in models B and C; for model B, migration of 5 individuals per generation out of Africa 60–50 ka; for model C, migration of 1.2 individuals per generation into Africa 100–50 ka. Relative likelihood is the proportion of simulations for which the age of the L3 node was less than or equal to 80 ka, relative to this value for model A.

Model		Relative likelihood
A	Late dispersal from Africa 55 ka	1.0
	ms 600 20000 -t 1.25 -l 3 200 200 200 -T -eN 0 10 -eG 0 56.27 -eG 0.05 0 -ej 0.1167 3 2 -en 0.1333 2 0.2 -ej 0.1833 2 1 -en 0.3333 1 1 45369 44223 59953	
B	Early dispersal 120 ka with gene flow from Africa ca 55 ka	0.6
	ms 600 20000 -t 1.25 -l 3 200 200 200 -T -eN 0 10 -eG 0 56.27 -eG 0.05 0 -ej 0.1167 3 2 -en 0.1333 2 0.2 -em 0.1667 2 1 100 -em 0.2 2 1 0 -en 0.2667 2 0.32 -en 0.3333 1 1 -ej 0.4 2 1 45539 39872 63447	
C	Early dispersal 120 ka with subsequent gene flow back into Africa	1.3
	ms 600 20000 -t 1.25 -l 3 200 200 200 -T -eN 0 10 -eG 0 56.27 -eG 0.05 0 -ej 0.1167 3 2 -en 0.1333 2 0.2 -em 0.1667 1 2 2 -en 0.2667 2 0.32 -em 0.3333 1 2 0 -en 0.3333 1 1 -ej 0.4 2 1 4984 41383 33507	



Box Figure 2. Distribution of the age of the L3 node in 20,000 simulations for each of the models listed in Table 2. The vertical dashed line at 80 Ka indicates the maximum estimated age of L3 in the human mtDNA tree. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

gene flow has been inferred in genome-wide analyses.^{39,94}

It has been argued that such alternative models can be discounted on the grounds that if they were true some non-L3 haplotypes would be found in present-day non-Africans.¹⁷ However, model B involves the fixation of migrant lineages from Africa within the ancestral non-African population following secondary gene flow. This occurs in mtDNA, but not necessarily at autosomal loci due to their much higher effective population size (N_e), and reflects the fact that mtDNA genealogies are potentially more susceptible to such migration and introgression events. Model C involves a recent coalescence of mtDNA lineages outside Africa combined with migration of one or more lineages back to Africa. Both of these possibilities are made more likely by a low ancestral non-African N_e . Further, whole-genome analyses have shown that the ancestors of present-day non-Africans experienced a profound reduction in autosomal N_e to below 3,000 for much of the period between MIS 5 and the Holocene.^{43,46}

To explore these possibilities, we simulated examples of each of the models in Box Fig. 1 using a coalescent approach and investigated the resulting distributions of L3 node age. Simulated mtDNA genealogies were generated for three populations representing present-day African, European, and Asian samples, with the European and Asian populations diverging at 35 ka, and the initial African/non-African split occurring at 55 ka in model A and 120 ka in models B and C. For model B, we simulated a short period of strong migration (5 individuals per generation) out of Africa from 60–50 ka, while model C featured an extended period of weaker back-migration (1.2 individuals per generation) into Africa from 100–50 ka. Full demographic parameters and simulation commands are listed in Table 2. For each model, we generated 20,000 simulations of 600 samples using ms⁹⁵; increasing the number of samples had a negligible effect on results since the vast majority of coalescent events occur recently. Conservatively, we took a present-day t_{gen} of 30 yr as valid for the whole of human prehistory.⁹⁶

In each simulation, the coalescent tree was inspected and the youngest node ancestral to all non-Africans and some Africans was identified as the node equivalent to L3. (Note that there will always be such a node in any genealogy, but under an arbitrary or unstructured demography it will often coincide with the global root.) Box Fig. 2 shows distributions of the age of this node for each model. Relative empirical likelihoods of $L3 \leq 80$ ka are given in Table 2.

The models simulated represent plausible demographic histories based on genetic and other evidence for human prehistory. They demonstrate the range of variation in the age of the L3 node that one might expect under similar scenarios. However, they are not formally fitted to the observed human mtDNA genealogy; indeed, a value of 80 ka or less is unlikely under all these models (only 9% of simulations under Model A). It would be possible to infer parameters maximizing this likelihood, but inference based on one node in a single genealogy would not be robust.

Nevertheless, these results show that alternative models can be constructed involving an early dispersal out of Africa for which a recent age for L3 is not substantially less likely than under an equivalent model of late dispersal. Without further evidence of the geographical extent and structure of human populations during this period, an absence of non-L3 haplotypes outside Africa today cannot be regarded as conclusive evidence against a dispersal of *Homo sapiens* out of Africa beginning by MIS 5. It is also worth noting that a more recent analysis incorporating ancient DNA estimated an age of 95–62 ka for L3,⁴³ representing a substantial overlap with MIS 5.

in point (Box 1). It has been argued that the chronology and spatial distribution of branches of the human

mtDNA and Y chromosomal trees are inconsistent with dispersal any earlier than ~60–50 ka.^{17,36,37} How-

ever, as Box 1 shows, this argument, which assumes straightforward correspondence between genealogical

trees and demographic history, is not valid under plausible alternative models of divergence, with gene flow between subpopulations over tens of millennia. Support for such models comes in part from recent evidence that much of the population structure in Africa is of surprisingly ancient provenance.³⁸ Further support comes from genome-wide inferences of a gradual divergence with ongoing gene flow between African and non-African ancestors during MIS 5.³⁹ Indeed, with a revised estimate of $0.5 \times 10^9 \text{ bp}^{-1} \text{ y}^{-1}$ for the nuclear genomic mutation rate, whole-genome demographic studies favor an older time scale and a more complex process of dispersal out of Africa.⁴⁰ Evidence of this rate has come primarily from sequencing studies of *de novo* mutations. Some concerns have been raised about the influence of false negatives on such data.⁴¹ However, not only have more than a dozen such studies now arrived at similarly low values,⁴² but independent evidence has also come from comparing ancient and modern human DNA.⁴³ The lower rate is more consistent with inferences for the timing of recent events such as the divergence of Native American and East Asian populations.³⁹

These considerations are not to dispute the continuing value of mtDNA as a source of information on human evolution, particularly for more recent events. It is still more widely sampled than are the autosomes (chromosomes 1–22) and more amenable to ancient DNA studies. mtDNA also has a smaller effective population size (N_e) (around one-quarter of the mean autosomal value, depending on certain demographic factors), meaning that patterns of diversity in mtDNA sequences respond more rapidly to demographic changes. Thus, mtDNA trees can be informative about more recent demographic history where there are numerous uncoalesced branches in the tree, albeit with the caveats previously mentioned. For example, the “star-like” topology of non-African branches of the mtDNA and Y chromosome trees around 50 ka^{44,45} suggests an acutely reduced non-African N_e at this time, as well as

rapid population growth following it, which may or may not correspond to a major migration event such as a population dispersal. This topology also coincides with the N_e minimum of the non-African bottleneck inferred from whole-genome analysis.⁴⁶ Future analyses combining widely sampled mtDNA, Y-chromosomal, and genome-wide data should provide a more powerful means of inferring recent demographic processes.

Returning to earlier events, the emerging picture is one in which by MIS 5 *Homo sapiens* existed within various subpopulations, differing in their size and degree of genetic contact, and perhaps distributed over a wide area. At least one of these included the ancestors of present-day non-Africans and was characterized by low N_e . Based solely on present-day genetic data, which has weak geographical resolution when looking distantly into the past, it is difficult to say how far one or more of these populations might have extended into Asia before ~60 ka. A major reason for this is the prevalence of subsequent migration and gene flow, not only within Eurasia, but also from Eurasia back into Africa and within Africa.^{47,48} Such events weaken the correlation between present and ancestral haplotype distributions and depend on ecological and environmental factors that are challenging to model.

It may therefore be that some of these questions can be resolved only by a combination of archeology and ancient DNA sequencing.⁴⁹ Ancient DNA has already been transformative in revealing interbreeding between *Homo sapiens* and other hominins, including Neanderthals, Denisovans, and perhaps other archaic populations.^{9,10,49} In particular, one episode of *Homo sapiens*-Neanderthal interbreeding has now been dated to 60–50 ka, based on the clear signature it left in the ancient genomes of MIS 3 individuals from Siberia.^{35,43} This has implications for the question of when *Homo sapiens* left Africa. For example, if it represents the earliest episode of interbreeding, and if we expect interbreeding to have begun as soon as humans left Africa, this finding would seem to

cast doubt on the hypothesis of an earlier human exodus. This finding also suggest that genetic signals of population divergence before 60 ka relate to substructure within Africa. However, there are alternative possibilities:

- (1) Since the method used to date introgression assumed only a single episode of gene flow, earlier episodes may have been undetected.
- (2) Neanderthals may have ranged farther north before ~70–50 ka, so that *Homo sapiens* encountered them only sometime after leaving Africa as part of a secondary *Homo sapiens* migration or Neanderthal expansion southward.
- (3) The vast majority of post-60-ka human lineages may descend from a second wave of *Homo sapiens* out of Africa at that time (model B in Box 1), in which case earlier episodes of interbreeding may have left a minimal genetic legacy.
- (4) Contact between *Homo sapiens* and Neanderthals may have occurred earlier but unproductively, perhaps due to low hybrid viability or fertility, or other reproductive obstacles.⁵⁰

ARCHEOLOGICAL EVIDENCE

Several dispersal models claim support from patterns in archeological and, particularly, lithic data (Figs. 1 and 2; Table 1). In evaluating the evidence underlying these claims, it must be recognized that multiple processes, in this case branching (cultural inheritance and spread), blending (cultural diffusion between populations), and convergence (independent reinvention), can produce similar forms of material culture (equifinality). The first two of these processes can alternatively be described as homology and the latter as analogy.

There are many examples of convergence in lithic technology. Particular care must be taken when likely drivers of independent reinvention, such as the constraints of hafting, exist. In other ways, however, archeological data can provide robust signals of dispersal. A key example relates to Australia, which, in contrast to Asia, with its multiple hominin species, was peopled, as far as is known, only by *Homo sapiens*.

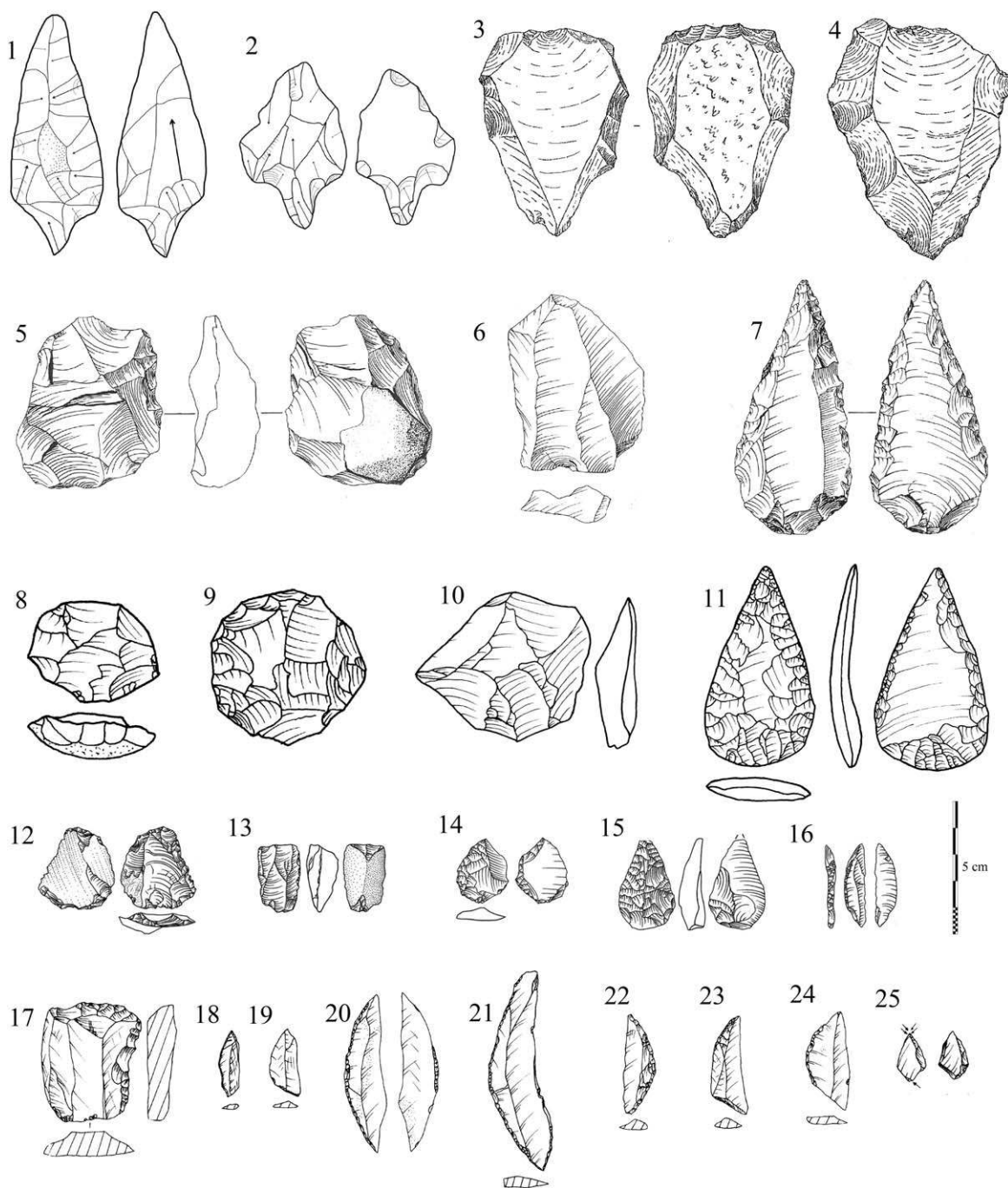


Figure 1. Selected lithics (stone tools) from East and North Africa for MIS 5 (1–11) and MIS 3 (12–25). 1–4: iconic MIS 5 Middle Paleolithic (Middle Stone Age) lithic types and techniques of North Africa; 1–2: tanged or pedunculated Aterian points, widely thought to have been hafted tools⁶⁸; 3, 4: “beaked” (“Nubian”) Levallois cores⁶²; 5–11: other common components of North (5–7, from Bir Tarfawi, Egypt)⁶⁴ and East (8–11, from BNS, Omo Kibish, Ethiopia)⁶³; African MIS 5 MP assemblages; 5, 8, 9: recurrent centripetal Levallois cores; 6, 10: centripetally prepared Levallois flakes; 7, 11: retouched points. Late MP cores (12, 13) and retouched points (14, 15) and backed microlithic (16) from Mochena Borago, Ethiopia, ~50 ka.⁵⁵ 17–25: Early Late Paleolithic (Later Stone Age) lithics from Enkapune Ya Muto, Kenya ~50–40 ka; 17: end and side retouched flake; 18–24: backed flakes or microliths; 25: burin.¹⁰³

Available data suggest that *Homo sapiens* had reached Australia before 50 ka.⁵¹ The Australian archeological record provides a key minimum age for dispersal out of Africa.

The Evidence of MIS 3 Dispersals

Various models cite archeological data as indicating the dispersal of *Homo sapiens* into Asia ~70–40 ka.

Most prominently, the appearance of new lithic technology and other aspects of material culture traditionally described as “Upper Paleolithic” in the Levant from ~47/45 ka has

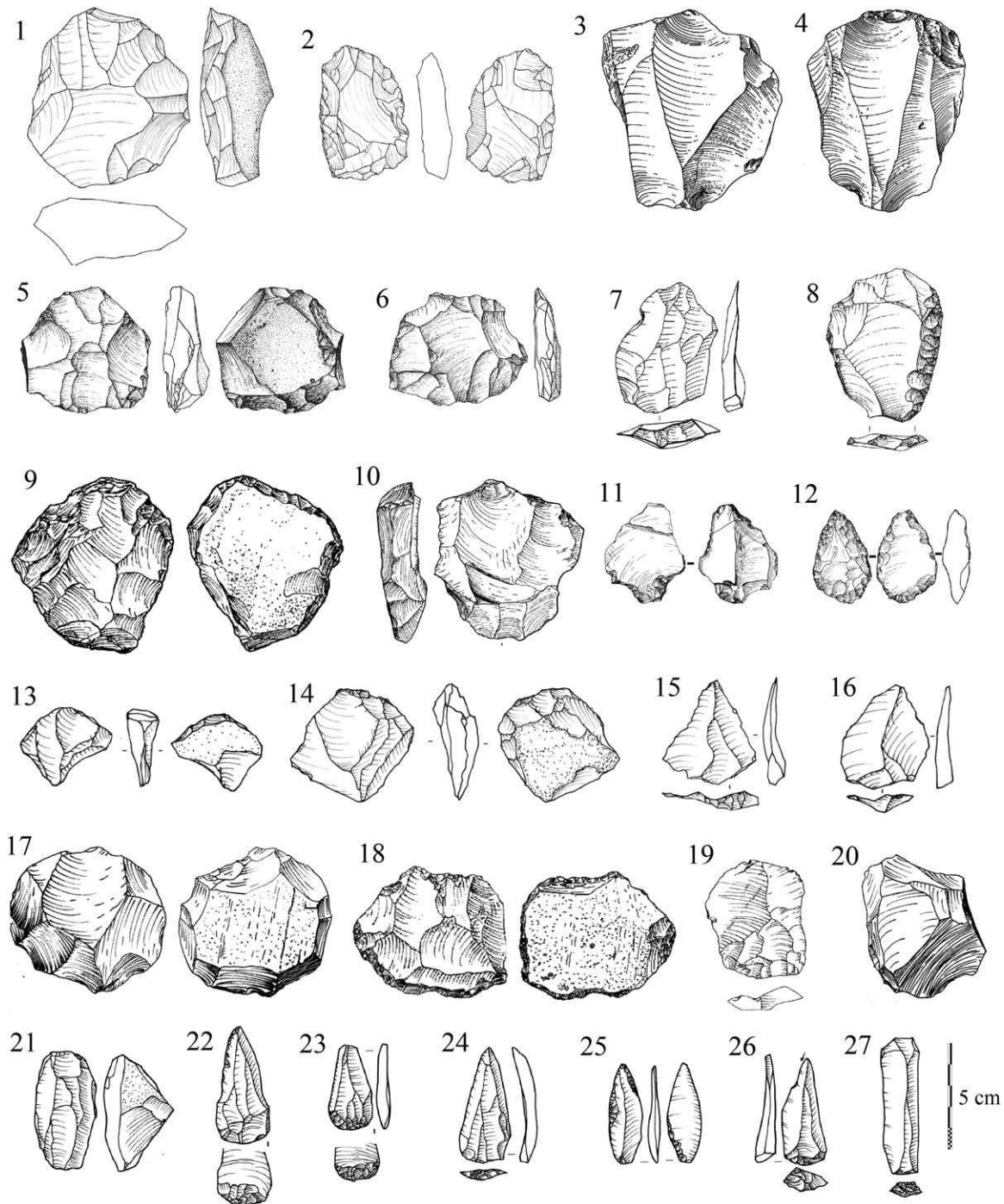


Figure 2. Selected lithics from Southwest and South Asia from MIS 5 (1–12) and MIS 3 (13–27). 1–4: Arabian Peninsula. 1: centripetally prepared preferential Levallois core, Jebel Faya, UAE, ~125 ka; 2: bifacially flaked tool, Jebel Faya¹⁰⁴; 3,4: beaked (or Nubian) Levallois cores from TH-59, Oman, probably MIS 5²⁰; 5–8: Qafzeh Cave, Israel, ~100–90 ka; 5: recurrent centripetal Levallois core; 6: centripetally prepared preferential Levallois core; 7: Levallois flake; 8: side retouched Levallois flake.⁶⁵ 9–12: MIS 5 lithics from Jwalapurum 22, India, ~75 ka. 9: recurrent centripetal Levallois core; 10: centripetally prepared preferential Levallois core; 11: tanged or pedunculated flake; 12: retouched point⁶⁶; 13–16, typical artifacts of the Levantine Late Middle Paleolithic, Dederiyeh Cave, Syria, ~60 ka. 13,14: unidirectional convergent Levallois cores; 15,16: Levallois points with unidirectional convergent preparation.¹⁰⁵ 17–20, Late Middle Paleolithic lithics from Jwalapurum 3 and 20, India, ~55–30 ka, 17: centripetally prepared preferential Levallois core; 18: recurrent centripetal Levallois core; 19, 20: Levallois flakes.⁶⁶ 21–27: Early Upper Paleolithic lithics from the Levant, ~40 ka. 21: blade core; 22–26: points; 27: blade.¹⁵

been seen as evidence of the rearrival of *Homo sapiens* from Africa (Fig. 2: 21–27).¹⁵ Key aspects of this include the hypothesis that this dispersal reflects the invention of projectile technology in Africa.¹⁵ Such developments perhaps gave *Homo sapiens* a selective advantage over Neanderthal populations in Eurasia. However, the extent to which this model can be generalized beyond the Levant is currently unclear.

Microlithic or geometric technologies were variably present throughout the African Middle Paleolithic (MP). (Here we use “Middle Paleolithic” to include the synonymous Middle Stone Age and “Late Paleolithic” as a way of describing assemblages traditionally designated as Upper Paleolithic, Later Stone Age, or Microlithic). Mellars and colleagues¹⁷ argue for dispersal into southern Asia by a coastal route before the origin of the Upper Paleolithic in the Levant. They cite the distribution of microlithic and geometric technologies around the Indian Ocean rim as providing evidence of a single dispersal of *Homo sapiens* out of Africa ~55–50 ka (for example, Fig. 1: 17–25). The Howiesons Poort (HP), emphasized by Mellars and colleagues,¹⁷ is an early example of technologies commonly described as microlithic or geometric that become temporarily a common part of assemblages. However, recent studies, emphasize the diversity of HP assemblages, for example in core reduction methods and in features of retouched tools.^{52–54}

In East Africa, microliths occur in low frequencies from around 50 ka and subsequently increase in frequency.⁵⁵ For example, a single complete crescent was found at Mochena Borago (Fig. 1: 16) within a pattern of general technological continuity. Earlier claims face taphonomic and chronological problems.⁵² The onset of the Late Paleolithic in East Africa appears to have been initially characterized by a reduction in the size of lithics and an increase in bipolar reduction. In South Asia, there also appears to be a gradual and complex transition from the Middle to Late Paleolithic.^{56–61} The early phase of the

Late Paleolithic in South Asia was dominated by blade and microblade production, with microlithic technology becoming widespread from ~38/35 ka. The oldest microlithic site in Sri Lanka, Fa Hien-lena, dating to ~38 ka, contains only nongeometric forms.⁵⁹

While these findings do not fit easily with the notion of microlithic technology as a unique marker of the dispersal out of Africa, Mellars and colleagues emphasize the similar range of shapes, such as crescents, lunates, and trapezoids, of some subsequent South Asian microliths and the earlier African forms.¹⁷ To Mellars and colleagues, these similarities in shape are best explained by branching and blending processes of cultural interaction and dispersal.

Advocates of the notion of dispersal from Africa at around 60–50 ka also cite the apparent distribution of “symbolic” artifacts such as beads and incised ostrich eggshell.¹⁷ Cited examples include Batadomba-lena at ~35 ka and Jwalapuram 9 at ~20–12 ka.^{58,59} Mellars and colleagues argue that older examples, as well as early examples of microlithic technology, have been concealed by sea-level rise.¹⁷

MIS 5 DISPERSALS

Archeological findings in southern Asia have been interpreted as indicating early dispersals of *Homo sapiens* out of Africa (that is, by MIS 5, ~130–75 ka) (Table 1). While the Middle Paleolithic in Europe is associated with Neanderthals, in Africa it not only temporally overlaps with most of the period in which *Homo sapiens* was present, but also characterizes the early expansion of *Homo sapiens* to the Levant.^{62–65} Given that available data indicate that humans were in Southeast Asia and Australia before the origin of the Late Paleolithic in Africa and Asia, there is a strong indication that at least an early phase of dispersal out of Africa was associated with MP lithic technology.^{66,67} Elucidating variability within MP technologies is therefore of great importance for understanding dispersal.⁶⁸

One recent model emphasizes the combination of Levallois, blade, and

façonnage reduction methods found at the Arabian site of Jebel Faya and claims that these are similar to features of the East and Northeast African Middle Paleolithic (Fig. 2: 1–2).¹⁹ An alternative model instead stresses the discovery of “beaked” (or “Nubian”) Levallois technology, previously best known from Northeast Africa (Fig. 1: 3–4), in Arabia (Fig. 2: 3–4).²⁰ The former emphasizes a rather broad combination of features; the latter highlights one aspect of technology that may represent convergent (independent) evolution. The notion that the “Nubian complex” is a spatially and temporally restricted technocomplex becomes problematic with the discovery of similar technologies from Mauritania to the Thar Desert via South Africa.⁶⁷ The distinctive “beaked” or “Nubian” cores were first described by Seligman,⁶² who thought that the shape of the median-distal ridge was similar to the shape of a tortoise beak. We propose use of the morphologically descriptive term “beaked” instead of “Nubian,” which implies an automatic association of this technology with Nubia; emerging evidence may be consistent with the convergent reinvention of this technology.

An alternative lithic Out-of-Africa signal may be the spread of East African technologies, with a trail of similar assemblages linking East Africa,⁶³ Northeast Africa,⁶⁴ the Levant,⁶⁵ and as far east as India by late MIS 5 (Fig. 1: 5–11, Fig. 2: 5–12).^{51,66} The search for an archeological “smoking gun” for dispersal out of Africa is challenged by the diversity of lithic technology within Africa before dispersal. Scerri and colleagues, for instance, have demonstrated spatially structured lithic variability in MIS 5 North Africa,⁶⁸ correlating with modeled ecozones rather than traditional “industrial” nomenclatures such as “Aterian” and “Nubian complex.” This finding is interpreted as indicating structured (subdivided) populations by MIS 5. Such inferences represent an important archeological finding that can be factored into models using genetic data.

The South Asian MP shows considerable technological continuity from later MIS 5 through MIS 3 (Fig. 2: 9–

12, 17–20),^{66,67} suggesting that hominin population continuity in the mosaic environments of South Asia occurred through the Toba super-eruption of 75 ka. It is possible, however, that there was also an earlier *in situ* Lower to MP transition, although this possibility requires further analysis. South Asian MP assemblages dating to MIS 5 feature beaked (“Nubian”) Levallois technology and other components common in the African record,^{66,67} but lack the kind of technology associated with Neanderthals in at least the Levant (Fig. 2: 13–16) and central Asia.⁵² Key reviews of Asian paleoanthropology include those by Denell,⁶⁹ who focused on the pre-MIS 5 period, and Rabett,⁷⁰ who addresses the post-MIS 5 period.

In the case of the Levant, MP technology is found alongside various indications of complex behavior, including deliberate burials, beads, and the use of ochre, features that arguably articulate the record more closely with that of Africa than Europe.^{24,71} Some of the earliest examples of such behavior, which are actually found at the non-African site of Skhul (~130–100 ka),⁷¹ and more robustly at the slightly younger site of Qafzeh (~100–90 ka), suggest that by at least MIS 5 *Homo sapiens* was capable of complex, including symbolic, behavior.^{72,73} Such behavior was expressed in a variable manner, perhaps in relation to environmental or demographic factors.⁷⁴ The current lack of evidence of symbolic behaviors in areas such as Arabia may reflect factors such as lack of research in a given area or the fact that most sites discovered consist of raw material procurement and early stage reduction localities.

ENVIRONMENTS AND DISPERSAL ROUTES

The final major component of debate over the dispersal of *Homo sapiens* out of Africa concerns the routes taken and how they correlate more widely with ecological conditions. Some have emphasized terrestrial dispersal routes.²⁷ For example, combining archeological and envi-

ronmental data for North Africa has shown that MP sites tend to be most technologically similar to nearby sites except where they were connected by rivers (see Box 2).⁶⁸ An alternative perspective hypothesizes that coastal routes were key.¹⁷

Environmental variation influences dispersal not only in terms of its effects on factors such as net primary productivity, which leads to demographic fluctuation, but also by opening and closing routes, such as through the generally arid Saharo-Arabian zone.^{75,76} The history of research cautions against directly correlating environmental and demographic processes. For example, paleoclimate data from Lake Malawi suggesting that “mega-droughts” occurred in sub-Saharan Africa has been cited as a key mechanism explaining the apparent dispersal out of Africa at around 60 ka.¹⁷ However, subsequent research has demonstrated that the MIS 5 mega-drought ended much earlier, by ~85 ka.⁷⁷

While numerous archives in the Saharo-Arabian belt attest to dramatic increases in humidity during periods such as MIS 5,^{75,76} early MIS 3 (~60–50 ka) also witnessed a significant humid phase in Arabia.⁷⁸ This MIS 3 wet period may have provided the context for a renewed phase of dispersal out of Africa and/or the expansion of refugial populations already within Arabia. The evidence of interior humidity and hominin occupations some distance from the coast in Arabia in MIS 3 suggests that a coastal route need not have been exclusively followed (Box 2). It also suggests that terrestrial dispersals need not have been limited to MIS 5.

Coastal Dispersal Models

Recent years have witnessed intensified debate about the role of coastlines in hominin evolution and dispersal.^{17,27,79–83} At one extreme, proponents of purely coastal routes see those routes as providing a mechanism for fast, directional, population expansion along an ecologically uniform coastal highway.¹⁷ According to this view, MIS 3 coastal regions were highly stable and pro-

ductive environments. Field data, however, remain minimal.

South African sites demonstrate the use of molluscs, fish, and sea mammals exploited from the seashore alongside terrestrial foods, but they lack evidence of offshore activity.⁸³ Most of these findings relate to MIS 5/4, but earlier examples may be concealed by sea level rise. The only other reported example of possible early coastal subsistence outside South Africa is the MIS 5 Eritrean site of Abdur,⁷⁹ where shells from shellfish apparently collected for food have been reported alongside stone tools and terrestrial mammals in a beach deposit. However, without further supporting details or evidence of other marine resource use, Abdur’s place in the record of Pleistocene coastal exploitation is unclear.⁸⁴ There is nothing in these findings to indicate that marine resources were uniquely associated with anatomically modern humans or that they supported marine-focused paleoeconomies. Other hominins, and even nonhominin primates, also exploited marine foods on the seashore.⁸⁵

Only in Sahul is there clear evidence of the conjunction of colonization, seafaring, and heavy dependence on marine resources during the Pleistocene. Occurring only in the archipelago environments of Wallacea and the Bismarck islands, this may reflect a unique combination of circumstances: abundant bamboo driftwood for rafts; an archipelago environment with favorable winds and currents where land is rarely out of sight; a depauperate island fauna and little available terrestrial food; a rich and varied supply of marine resources; and uplifted coastlines preserving caves occupied during low sea level above the present shoreline.^{86–89} Once humans reached landfall in Sahul, they rapidly moved inland, leaving little evidence of prolonged coastal settlement even on the tectonically uplifted coastlines of northern New Guinea.

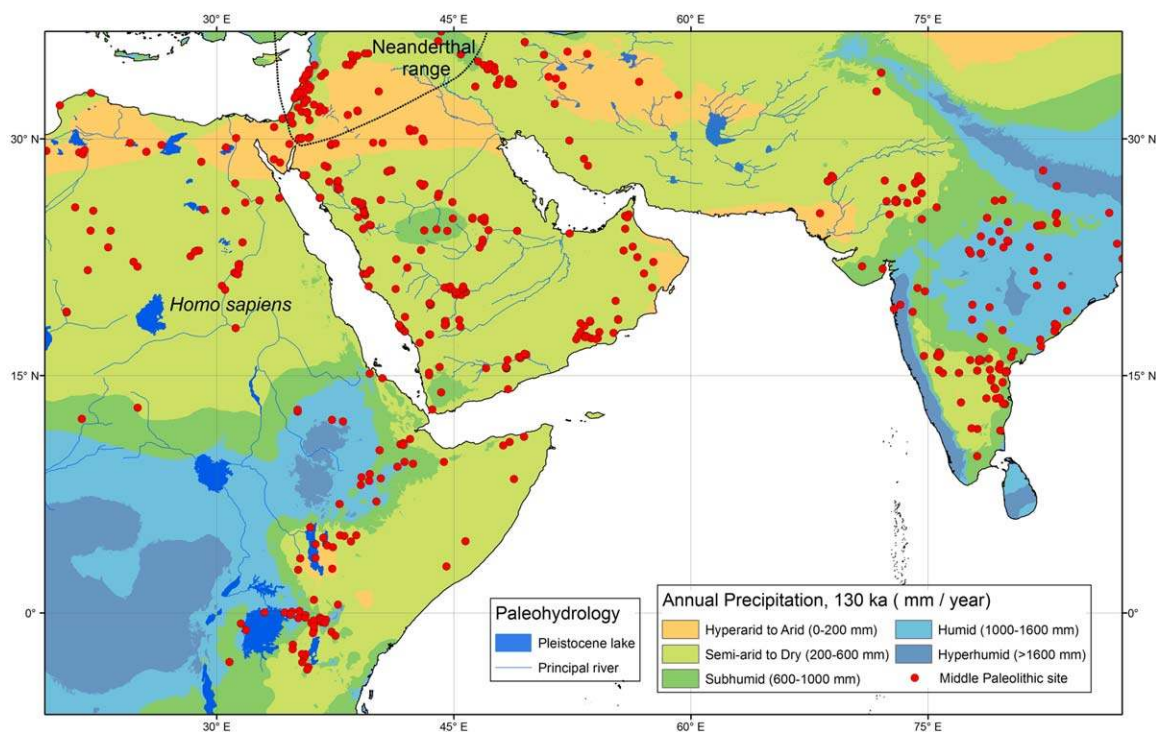
It is possible that analogous conditions existed on paleoshorelines elsewhere around the Indian Ocean, but that these have been submerged by sea level rise.¹⁷ Testing this hypothesis requires surveys both underwater

Box 2. Paleoclimate, Paleohydrology and the Distribution of Middle Paleolithic Sites

The distribution of MP sites in the Saharo-Arabian belt provides insights into Late Pleistocene landscape use, given that at least the early phase of dispersal out of Africa was associated with MP toolkits. As

modeled 130 ka precipitation data derived from the down-scaled Community Systems Model (CCSM 3) data.^{100,101} Box Fig. 1 shows that most MP sites in this region occur in areas of increased rainfall; how-

ing has shown that the number of recorded MPs declines considerably as distance from major rivers increases, with 74% of MP sites within 30 km of large paleodrainage systems.⁹⁹ This is ongoing research,



Box Figure 1. The distribution of Middle Paleolithic sites across East Africa, the Saharo-Arabian belt, and India, plotted on a modeled precipitation map for the last interglacial (MIS 5) with positions of major paleolakes (dark blue areas) and paleorivers, which form extensive riparian corridors (blue lines). The Neanderthal range line shows the estimated extent of Neanderthal dispersal from the north. The map shows that Middle Paleolithic sites are commonly located in interior regions and that their presence in typically arid areas can be explained by the humid climate conditions of periods such as MIS 5, which activated paleohydrological networks and potentially transformed major deserts into savannah grasslands and shrublands (green areas) containing numerous freshwater lakes and rivers. The paucity of sites in Pakistan and eastern Iran almost certainly reflects research history rather than a real pattern. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

shown in Box Fig. 1, vast areas of the generally arid Saharo-Arabian belt were potentially transformed into grassland and savanna environments by increased rainfall during several humid periods, including those of MIS 5. Box Fig. 1 combines paleohydrological data^{63,97–99} with

ever, it also demonstrates the persistence of an arid desert belt even during times such as MIS 5e. Paleorivers formed potentially crucial corridors (and filters) through these arid environments, as demonstrated for the Sahara during MIS 5e.^{68,102} In Arabia, paleohydrological model-

but initial results are congruent with hypotheses that fluvial networks formed important dispersal corridors, as Arabian MP sites are generally located much closer to major paleorivers than would be expected if they were randomly distributed.⁹⁹

and on land proximal to coastlines.^{81,89} A broad delineation of the continental shelf around the Indian Ocean approximating a sea level position of –100 m at the maximum

Late Pleistocene regression highlights the considerable variability in the width and topography of the coastal shelf, and therefore in the area and nature of Pleistocene land-

scapes that have been submerged (Fig. 3). Intensive surveys in some areas proximal to narrow coastal shelves, such as the Dhofar coast of Oman (Fig. 3D), have failed to reveal

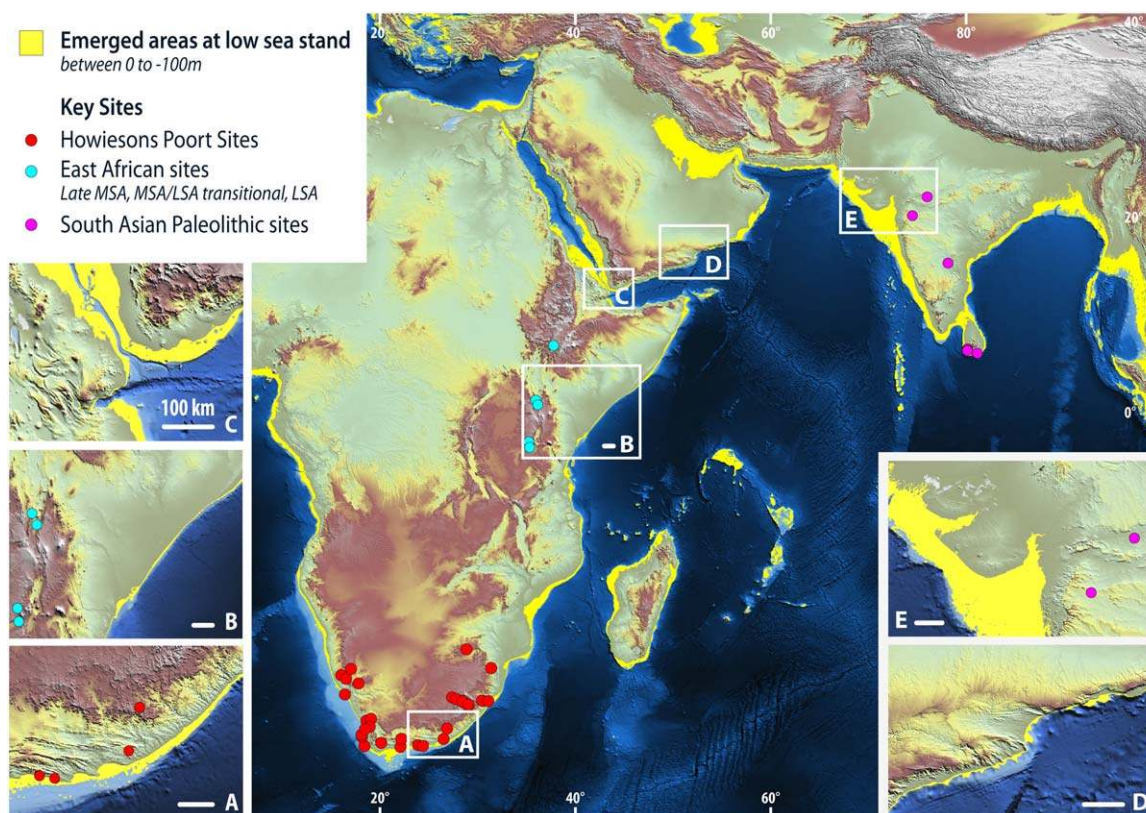


Figure 3. Map showing topography and bathymetry (SRTM30PLUS). Areas in yellow correspond to currently submerged land that would have been exposed when sea level was $\sim 100\text{m}$ lower than present. Colored dots correspond to key archeological sites (Howiesons Poort, MSA/LSA transitional, and South Asian Late Paleolithic) emphasized by the model of Mellars and coworkers.¹⁷ The inserts show that the landscape can be very different from place to place and that there is no “typical” coastal environment. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

Late Pleistocene marine-focused archeology.²⁰ The presence of Lower Paleolithic and Neolithic material indicates that this absence is not simply a question of preservation. Parts of the coastal margin of eastern Arabia have experienced tectonic uplift, including during the Pleistocene,⁹⁰ but no archeological evidence consistent with the expectations of purely coastal models has been identified on these landforms either. Conversely, a large area of submerged coastal shelf occurs between East Africa and southwest Arabia, making it a key area for further survey both underwater and on neighboring land.^{89,91}

Coastal regions are extremely variable both in space and through time. Some regions are attractive as much because of favorable conditions for proximal terrestrial resources, including abundant water supplies, river estuaries, equable climate conditions, a long growing season, and

great ecological diversity, as for their marine resources. Others are barren or inaccessible because of the encroachment of steep mountain ranges, estuarine mudflats, thick forest, or desert.

Examples of Holocene *Homo sapiens* marine specialist economies are rare. They typically occur in archipelago environments with highly productive marine resources accessed through advanced technologies, including seafaring and food storage, often at high latitudes alongside unproductive or inaccessible terrestrial environments (notably in Norway, the northwest coast of North America, and Tierra del Fuego). The possibility that similar economies existed on now-submerged Pleistocene shorelines cannot be ruled out, but in any case such economies are likely to have been very patchy in their distribution, as in the Holocene. To the extent that marine resources were exploited, they are likely to have

been combined with terrestrial resources and the use of the hinterland through seasonal movements or in symbiosis with inland communities, the more typical pattern in Holocene ethnographic and archeological records.⁸¹

Archeological sites that appear close to the coast on large-scale maps are often much further inland. For instance, the average distance from the modern coast of the 31 Howiesons Poort (HP) sites we analyzed is $\sim 105\text{ km}$, despite a research bias toward coastlines. HP sites are up to 350 km from the modern coast (Rose Cottage Cave). Post-HP sites in South Africa are typically even further from the coast than are HP sites. The East African sites that have been argued to support a coastal dispersal $\sim 55\text{ ka}$ ¹⁷ are, on average, 600 km from the coast; early South Asian Late Paleolithic sites are also typically far inland. In Sri Lanka, early microlithic sites are

TABLE 3. Tabulation of the Relative Strength of Fossil and Archeological Evidence of the Presence of *Homo sapiens* in Southern Asia and Australia for selected time periods^a

Date (ka)	Levant		Arabia		South Asia		Southeast Asia		Australia	
	Fossil	Arch.	Fossil	Arch.	Fossil	Arch.	Fossil	Arch.	Fossil	Arch.
40	+++	+++		+		+++	+++	+++	+++	+++
50	+	++		+		++	+++	++	+	+++
60	++	-		+		++	++			+
75	+	++		++		++	+		-	-
100	+++	+++		++		+	+		-	-
140	+	+							-	-

^a+++ = strong evidence, ++ = moderate evidence, + = weak evidence, - = relatively good evidence of absence, gray cell = uncertain/insufficient information to assign to one of these categories. For details see text.

generally inland and clearly demonstrate terrestrial subsistence, particularly the hunting of monkeys.⁵⁹

Much remains to be learned about the role of coastal or marine resources and habitats in the Pleistocene. However, evidence of a dramatic adaptation to coastal ecologies and dispersal along coasts at or before ~50 ka is currently lacking. It is likely that coastlines provided patches of favorable habitats, but that these were discontinuous in space and time. Rather than limiting dispersal models to the strictly dichotomous “interior” or “coastal,” we suggest that, alongside a range of other Late Pleistocene habitats, from the semi-arid to rainforests, the use of coastal ecozones is best seen as part of the behavioral flexibility of *Homo sapiens*.

DISCUSSION AND CONCLUSIONS

Our review of evidence relating to the timing and routes of dispersal of *Homo sapiens* out of Africa shows that fossil, genetic, and archeological data are currently consistent with several different models. There is much more uncertainty in the timing and character of this dispersal than is generally suggested by those who argue that the first successful dispersal, occurred ~50 (±10) ka.^{1,14,17} Uncertainties remain about the extent of cultural and biological continuity in *Homo sapiens* populations outside Africa from MIS 5 onward, as well as about the meaning of the

major cultural and demographic changes around 50 to 30 ka.

We suggest that accumulating data increasingly support a hybrid model whereby early expansions were essentially swamped by subsequent ones. In terms of dispersal routes, we suggest that populations employed behavioral flexibility and adaptation to use a range of different ecologies, including interior savannahs and the coast. Accumulating evidence of early population structure and multiple population interactions indicates that simple models for the dispersal process are no longer sufficient. A key point is that the Asian paleoanthropological record remains extremely poor, as illustrated by the recent discovery of cave paintings dating to at least 40 ka in Indonesia.⁹²

Further work is needed to understand what constraints genetic and archeological data place on models of ancestral population dispersal across the Middle East and South Asia. We have shown that inferences from single-locus genetic data need to be based on an understanding of the relationship between demography and genealogical stochasticity, as embodied in coalescent or other population genetic models. Just as archeology has largely, but not entirely, transcended the “culture-history” approach, according to which pottery and tool types were simplistically seen as direct proxies for populations, so genetic analyses must avoid the “gene-history = population history” paradigm. Like-

wise, similarities between lithic assemblages, as well as other sorts of archeological data, can be explained by different mechanisms. A strong archeological argument for dispersal would involve the correlated appearance of a package of several elements of material culture. It is clear that many key cultural features evolved convergently, among them Levallois and blade technology, as well as tangling or pedunculation. We interpret available data as indicating the repeated and independent evolution of microlithic technology, but acknowledge that testing this, as well as notions of early dispersals with Middle Paleolithic technology, requires comparative analyses of assemblages in Africa and Asia. Quantitative analysis of attributes are one method that, critically, can derive technological insights from typologically indistinct artifacts.^{54,68}

Different regions have different strengths and weaknesses in determining the presence of *Homo sapiens* (Table 3). The Levant seems to feature a genuine occupational hiatus. The data from Arabia remain somewhat ambiguous, with the strongest archeological evidence consisting of MIS 5 lithics displaying similarities to African and Levantine material associated with *Homo sapiens* fossils, while post-MIS 5 Arabian lithics are culturally ambiguous.²⁶ In South Asia, fossil data are currently absent before ~35 ka, while archeological data provide moderate indications of the presence of *Homo sapiens* from MIS 5.^{66,67} In Southeast

Asia, the archeological data are ambiguous regarding the presence of *Homo sapiens* until ~50 ka at sites such as Niah Cave.⁷⁰ A series of earlier fossils from across Southeast Asia provide possible support for the presence of *Homo sapiens* back to ~100 ka, and more securely to 70/60 ka.^{28,29} In Australia, archeological data indicate the presence of *Homo sapiens* by ~50 ka, with the earliest secure fossil evidence dating to ~45 ka. Cumulatively, these data demonstrate that *Homo sapiens* were in Southwest Asia by ~120 ka and Southeast Asia by ~50 ka. The archeological and fossil data between these points can currently be interpreted in different ways and, as we have outlined here, genetic data have been subject to questionable interpretations that require explicit modeling to be formally tested.

A number of predictions can be made from various models and tested in future research. Regarding the question of whether *Homo sapiens* successfully dispersed into Asia before ~60 ka, several hypotheses and expectations can be posed. These include the discovery of pre-60 ka *Homo sapiens* fossils in Asia outside the Levant, as well as the demonstration of similarities in material culture reasonably explained by branching or blending in Africa and Asia before 60 ka. We expect further analyses of the genomic divergence between African and non-African ancestors to reveal signals of gene flow and population substructure at this time and for ancestral demography inferred from genetic data outside Africa to reflect dispersal into Asia from MIS 5.

A difficulty in inferring the routes and chronology of *Homo sapiens*' dispersal out of Africa is that it requires integration of many different sources of information, each with its own ambiguities and assumptions. In addition, quite distinct processes can generate very similar patterns of variation in both genetic and archeological data (equifinality). If dispersal out of Africa occurred in several waves, then it was neither exclusively "early" nor "late," but both. Clarification of this important issue requires better cross-disciplinary understanding and

the formulation of clear hypotheses that make explicit predictions about patterns in different types of data. Enhancement of the southern Asian fossil and archeological records remains critical, alongside the application of more ancient DNA sequencing. The interpretation of such future findings will most robustly be achieved within the context of multi-disciplinary collaborations.

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