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Rethinking the dispersal of *Homo sapiens* out of Africa

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Current fossil, genetic and archaeological 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 archaeological, 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.

Background

A variety of dispersal models (Table 1) address the period between the widely accepted African origin of *Homo sapiens* by around 200–150 thousand years ago (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 to these discussions.

Whereas earlier models focused on assessing the geographical origins of our species based on fossil data, more recent approaches seek to combine fossil, genetic, archaeological and paleoenvironmental data to inform on 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) timeframes (Table 1). This is, however, 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.

table 1 about here

Fossil evidence

Hominin fossil remains provided the initial foundations for the Out of Africa model.³ Future fossil discoveries in South Asia have the potential to radically transform our understanding of the dispersal of *Homo sapiens* out of Africa. Early *Homo sapiens* was morphologically variable.^{4,21} Traits that characterize *Homo sapiens* include neurocranial globularity, a supraorbital torus divided into central and lateral portions, face retreated below the forepart of the brain, a bony chin even in infants, a gracile tympanic bone, the absence of the iliac pillar, and a short and 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*. However, Omo-Kibish 2, which is believed to be of similar age, is much more archaic.³ Given small sample sizes, it is difficult to tell if the variation of early *Homo sapiens* represents intrapopulation variation, or the existence of 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 43/42 ka²², 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/crust covering the calvaria and hence are minimum dates and the specimen may be considerably older, and/or 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 is consistent with archaeological discoveries in suggesting that in the Late Pleistocene, reliably dated Neanderthals are only present in the Levant after MIS 5, when *Homo sapiens* appear to be absent, possibly aside from the Manot Cave cranium.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 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 reviews the fossil record for *Homo sapiens* between Arabia and Australia.²⁵ The oldest South Asian fossils found date to ~33-30 ka, from the Sri Lankan cave of Fa Hien. 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 suggested by the Upper Paleolithic model, 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 earlier than previously thought in Southeast Asia. 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, but these have produced taxonomically ambiguous specimens from sites with often poor stratigraphic and chronological control.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 for 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, and 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 for pervasive gene flow and admixture between populations.^{9,10,34,35} The relationship between genetic ancestry and demographic history is less straightforward than was often assumed by many, 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 whose shape is only weakly constrained by demography, and whereas 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 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} However, as Box 1 shows, this argument assumes a straightforward correspondence between genealogical trees and demographic history, and is not valid under plausible alternative models of divergence with gene flow between subpopulations over tens of millennia. Support for such models comes from recent evidence that much of the population structure in Africa is of surprisingly ancient provenance,³⁸ and 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 timescale and more complex process of dispersal out of Africa.⁴⁰ Evidence for this rate has come primarily from sequencing studies of *de novo* mutations, and some concerns were raised about the influence of false negatives on such data.⁴¹ However, not only have over a dozen such

studies now arrived at similarly low values,⁴² independent evidence has also come from comparing ancient and modern human DNA,⁴³ and 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

box I here

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 the autosomes (chromosomes 1-22), and more amenable to ancient DNA studies. It 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 mentioned above. For example, the ‘star-like’ tree 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 and rapid population growth following it, which may or may not correspond to a major migration event such as a population dispersal. It 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 a number of subpopulations, varying 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 .

How far one or more of these populations might have extended into Asia before ~60 ka is a difficult question to answer with inferences based solely on present-day genetic data, which has weak geographical resolution when looking distantly into the past. 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 which are challenging to model.

It may therefore be that some of these questions can be resolved only by a combination of archaeology 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, and suggest that genetic signals of population divergence prior to 60 ka relate to substructure within Africa. However, there are alternative possibilities:

- (a) Since the method used to date introgression assumed only a single episode of gene flow, earlier episodes may have been undetected.

- (b) Neanderthals may have ranged further north prior to ~70-50 ka, such that *Homo sapiens* encountered them only sometime after leaving Africa, as part of a secondary *Homo sapiens* migration or Neanderthal expansion southward.
- (c) 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 minimal genetic legacy.
- (d) *Homo sapiens*–Neanderthal contact may have occurred earlier but unproductively, perhaps due to low hybrid viability or fertility, or other reproductive obstacles.⁵⁰

Archaeological evidence

Several dispersal models claim support from patterns in archaeological, and particularly lithic (Figures 3 and 4), data (Table 1). In evaluating the evidence underlying these claims it must be recognized that multiple processes can produce similar forms of material culture (equifinality), namely: 1) branching (cultural inheritance and spread), 2) blending (cultural diffusion between populations), and 3) convergence (independent re-invention). The former two 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 re-invention exist, such as the constraints of hafting. In other ways, however, archaeological data can provide robust signals of dispersal. A key example relates to Australia, which was – as far as is known – only ever peopled by *Homo sapiens*, in contrast to the multiple hominin paleospecies of Asia. Available data suggest that *Homo sapiens* had reached Australia before 50 ka.⁵¹ The Australian archaeological record provides a key minimum age for dispersal out of Africa.

The evidence for MIS 3 dispersals

A number of models cite archaeological 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 being 'Upper Paleolithic' in the Levant from ~47/45 ka has been seen as evidence for the (re)arrival of *Homo sapiens* from Africa (Fig. 4: 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. The extent to which this model can be generalized beyond the Levant is, however, currently unclear.

figure 3 here

Microlithic/geometric technologies were variably present throughout the African Middle Paleolithic (MP) (here we use the term Middle Paleolithic to include the synonymous Middle Stone Age, while we use Late Paleolithic as a way of describing assemblages traditionally described as Upper Paleolithic, Later Stone Age or Microlithic). Mellars and colleagues argue for dispersal into southern Asia by a coastal route before the origin of the Upper Paleolithic in the Levant.¹⁷ They cite the distribution of microlithic and geometric technologies around the Indian Ocean rim as providing evidence for a single dispersal of *Homo sapiens* out of Africa ~55-50 ka (e.g. Fig 3: 17-25). The Howiesons Poort (HP), emphasized by Mellars and colleagues,¹⁷ represents an early example of technologies commonly described as microlithic/geometric become (temporarily) a common part of assemblages. However, rather than simply representing a homogenous technological repertoire, recent studies emphasize the diversity of HP assemblages, for example in core reduction methods and in features of retouched tools.^{53,54}

In East Africa microliths occur in low frequencies from around 50 ka – e.g. a single complete crescent at Mochena Borago (Fig. 3: 16), within a pattern of general technological continuity – and subsequently increase in frequency.⁵⁵ Earlier claims face taphonomic and chronological problems.⁵² The onset of the Late Paleolithic in East Africa appears to be 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 the 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 non-geometric 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 (e.g. crescents, lunates, trapezoids, etc.) of some subsequent South Asian microliths to 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.

The notion of dispersal from Africa at around 60-50 ka also cites the apparent distribution of ‘symbolic’ artefacts, such as beads and incised ostrich eggshell.¹⁷ Cited examples include Batadomba-lena at ~35 ka and Jwalapurum 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

Archaeological findings in southern Asia have been interpreted as indicating early (i.e. by MIS 5, ~130-75 ka) dispersals of *Homo sapiens* out of Africa (Table 1). While in Europe the Middle Paleolithic is associated with Neanderthals, in Africa it

temporally overlaps with most of the period in which *Homo sapiens* are present, and also characterizes their early expansion to the Levant. 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. Elucidating variability *within* MP technologies is therefore of great importance for understanding dispersal.

figure 4 here

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 4: 1-2).¹⁹ An alternative model instead stresses the discovery of ‘beaked’ (or ‘Nubian’) Levallois technology, previously best known from Northeast Africa (Fig. 3: 3-4), in Arabia (Fig 4: 3-4).²⁰ The former emphasizes a rather broad combination of features, and the latter highlights one aspect of technology, which *may* represent convergent (independent) evolution. The notion that the ‘Nubian Complex’ is a spatially and temporally restricted technocomplex is problematized by the discovery of similar technologies from Mauritania to the Thar Desert, via South Africa.⁶⁰ 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 the use of the morphologically descriptive term ‘beaked’ instead of the term ‘Nubian’ which implies an automatic association of this technology with Nubia, whereas emerging evidence may be consistent with the convergent re-invention 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. 3: 5-11, Fig. 4: 5-12).^{51,66} The search for an archaeological ‘smoking gun’ for dispersal out of Africa is challenged by the diversity of lithic technology within Africa prior to dispersal. Scerri and colleagues, for instance, demonstrate spatially structured lithic variability in MIS 5 North Africa,⁶⁸ correlating with modeled ecozones rather than traditional ‘industrial’ nomenclatures (e.g. ‘Aterian’, ‘Nubian Complex’). This data is interpreted as indicating structured (sub-divided) populations by MIS 5. Such inferences represent an important archaeological 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. 4: 9-12, 17-20),^{66,67} suggesting hominin population continuity in the mosaic environments of South Asia occurred through the Toba super-eruption of 75 ka. It is, however, possible 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} while lacking the kind of technology associated with Neanderthals in at least the Levant (Fig. 4: 13-16) and central Asia.⁵² Key recent reviews of Asian paleoanthropology include Dennell,⁶⁹ who focuses on the pre-MIS 5 period, and Rabett, who addresses the post-MIS 5 period.⁷⁰

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 which arguably articulate the record more closely with that of Africa than Europe.^{24,71} Some of the earliest examples of such behaviors 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). Such data suggests that by at least MIS 5 *Homo sapiens* were capable of complex (including symbolic) behavior.⁷²⁻⁷³ These were expressed in a variable manner, perhaps in relation to environmental or demographic factors.⁷⁴ The current lack of evidence for symbolic behaviors in areas such as Arabia may reflect factors such as a lack of research in this area and the fact 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 archaeological and environmental 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

box 2 here

Environmental variation influences dispersal both in terms of its effects on factors such as net primary productivity, leading 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, palaeoclimate data from Lake Malawi suggests that ‘mega-droughts’ occurred in sub-Saharan Africa and has been cited as a key mechanism explaining the apparent dispersal out of Africa at around 60 ka.^{17,23}

However, subsequent research has demonstrated the end of the MIS 5 mega-drought 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,^{74,75} early MIS 3 (~60-50 ka) also witnessed a significant humid phase in Arabia.⁷⁷ 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 for 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 them as providing a mechanism for fast, and directional, population expansion along an ecologically uniform coastal highway.¹⁷ According to this view, MIS 3 coastal regions were highly stable and productive environments. Field data, however, remains minimal.

South African sites demonstrate the use of molluscs, fish and sea mammals exploited from the seashore alongside terrestrial foods, but lack evidence for 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 apparently collected for food have been reported alongside stone tools and terrestrial mammals in a beach deposit. However, without further supporting details, and no evidence of

other marine resource usage, 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 supported marine-focused paleoeconomies. Other hominins, and even non-hominin primates, also exploited marine foods on the seashore.⁸⁵

Only in Sahul is there clear evidence for the conjunction of colonization, seafaring and heavy dependence on marine resources in the Pleistocene. This occurs 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, and left 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 on land proximal to coastlines and underwater.^{81,89} A broad delineation of the continental shelf around the Indian Ocean approximating a sea level position of -100m 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 landscapes that have been submerged (Figure 6). Intensive surveys in some areas proximal to narrow coastal shelves, e.g. the Dhofar coast of Oman (Figure 6D) have failed to reveal Late Pleistocene marine-focused archaeology.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 archaeological 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 – abundant water supplies, river estuaries, more equable climate conditions, a longer growing season, and greater ecological diversity – as for their marine resources. Others are barren or inaccessible because of encroachment of steep mountain ranges, estuarine mudflats, thick forest or desert.

figure 6 about here

Examples of Holocene *Homo sapiens* marine specialist economies are rare, and 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). Whether similar economies existed on now-submerged Pleistocene shorelines cannot be ruled out, but in any case they 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 archaeological records.⁸¹

Archaeological sites that appear close to the coast on large-scale maps are often much further inland than implied. For instance, the average distance from the modern coast of the 31 Howiesons Poort sites we analyzed is ~105 km, despite a research bias towards 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 HP sites. The East African sites argued to support a coastal dispersal ~55 ka,¹⁷ are on average 600 km from the coast, and early South Asian Late Paleolithic sites are also typically far inland. In Sri Lanka, early microlithic sites are generally inland and clearly demonstrate terrestrial subsistence, particularly the hunting of monkeys.⁵⁹

Much remains to be learned about the role of coastal/marine resources and habitats in the Pleistocene. However, evidence for 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 the use of coastal ecozones is better seen as part of the behavioral flexibility of *Homo sapiens*, alongside a range of other Late Pleistocene habitats, from the semi-arid through to rainforests.

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 archaeological data are currently consistent with several different models. There is much more uncertainty in the timing and character of this dispersal process than proponents of the first successful dispersal occurring ~50 (± 10) ka generally suggest.^{1,14,17} **Uncertainties remain about the extent of cultural and biological continuity in *Homo sapiens* populations outside Africa from MIS 5 onwards and 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 largely swamped by subsequent ones. In terms of dispersal routes we likewise suggest that populations employed behavioral flexibility and adaptation to utilize a range of different ecologies, including interior savannahs and the coast. Accumulating evidence for 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 are placed on models of ancestral population dispersal across the Middle East and South Asia by genetic and archaeological data. 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 archaeology has largely, but not entirely, transcended the ‘culture-history’ approach, where pottery and tool types were simplistically seen as direct proxies for populations, so genetic analyses must avoid the ‘gene-history = population history’ paradigm.** Likewise, similarities between lithic assemblages – and other sorts of archaeological data – can be explained by different mechanisms, and a strong archaeological 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 – including Levallois and blade technology, as well as tanging/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 attribute analyses represent one method that, critically, can derive technological insights from typologically indistinct artefacts.^{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 remains somewhat ambiguous, with the strongest archaeological 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 is currently absent before ~35 ka, while archaeological data provides moderate indications for the presence of *Homo sapiens* from MIS 5.^{66,67} In Southeast Asia the archaeological data is ambiguous on the presence of *Homo sapiens* until ~50 ka at sites such as Niah Cave,⁷⁰ while 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 archaeological data indicates 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 archaeological and fossil data between these points can currently be interpreted in different ways, and as we have outlined in this paper genetic data has 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, and the

demonstration of similarities in material culture reasonably explained by branching/blending in Africa and Asia pre-60 ka. We would 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. Additionally, a number of quite distinct processes can generate very similar patterns of variation in both genetic and archaeological data (equifinality). If dispersal out of Africa occurred in several waves then it was neither exclusively ‘early’ nor ‘late’, but rather 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. The enhancement of the southern Asian fossil and archaeological records remain critical, alongside the application of more ancient DNA sequencing. The interpretation of such future findings will most robustly be achieved within the context of multidisciplinary collaborations.

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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 (N.B., key references may considerably postdate the initial formulation of particular models).

Table 2. Tabulation of the relative strength of fossil and archaeological evidence for the presence of *Homo sapiens* in southern Asia and Australia for selected time periods. +++ = strong evidence, ++ = moderate evidence, + = weak evidence, - = relatively good evidence of absence, grey cell = uncertain/insufficient information to assign to one of these categories. For details see text.

Table 3. 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 prior to 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.

Table 1

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 subsequently dispersed from.	6
Multiregional model	Throughout the Pleistocene	<i>H. sapiens</i> evolved in several parts of the world simultaneously, 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 artefacts.	17
Variants of Early Onset Dispersal Model			
Early onset multiple dispersal model	Beginning in MIS 5 (~125-75 ka), also MIS 3 (~55-45 ka) key	Multiple dispersals out of Africa, associated with climatic 'windows of opportunity'. Early dispersals associated with MP	2,18

		technology.	
'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 Nubian Levallois technology in Arabia.	20

Table 2

Model	Relative likelihood
A Late dispersal from Africa 55 ka ms 600 20000 -t 1.25 -I 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	1.0
B Early dispersal 120 ka with gene flow from Africa c. 55 ka ms 600 20000 -t 1.25 -I 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	0.6
C Early dispersal 120 ka with subsequent gene flow back into Africa ms 600 20000 -t 1.25 -I 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	1.3

Table 3

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

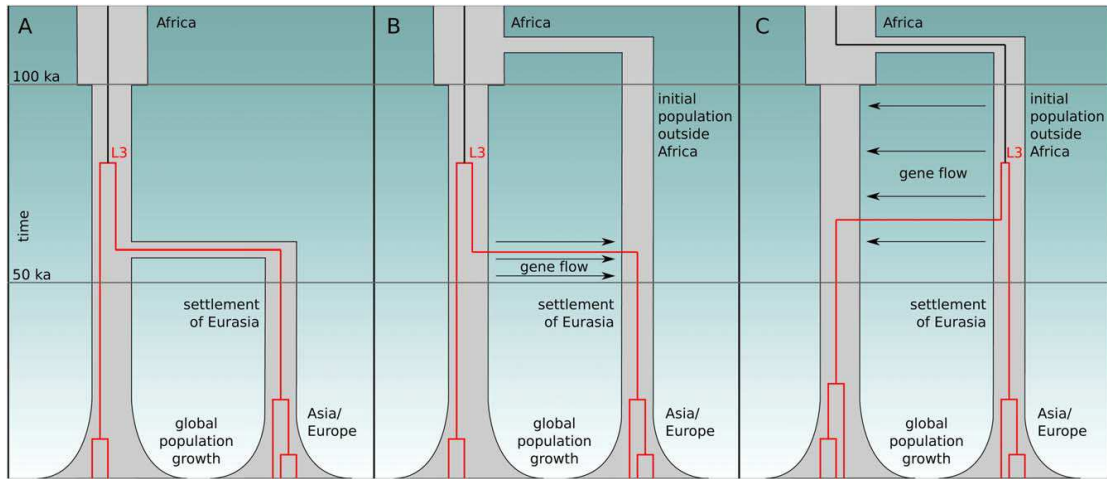


Figure 1 (in box 1). Alternative models of the relationship between the mtDNA genealogy and demographic history. Models B and C illustrate the possibility of an early divergence of African and non-African ancestors with subsequent gene flow, potentially congruent with fossil and archaeological evidence for a dispersal of *Homo sapiens* out of Africa ca. 100 ka.

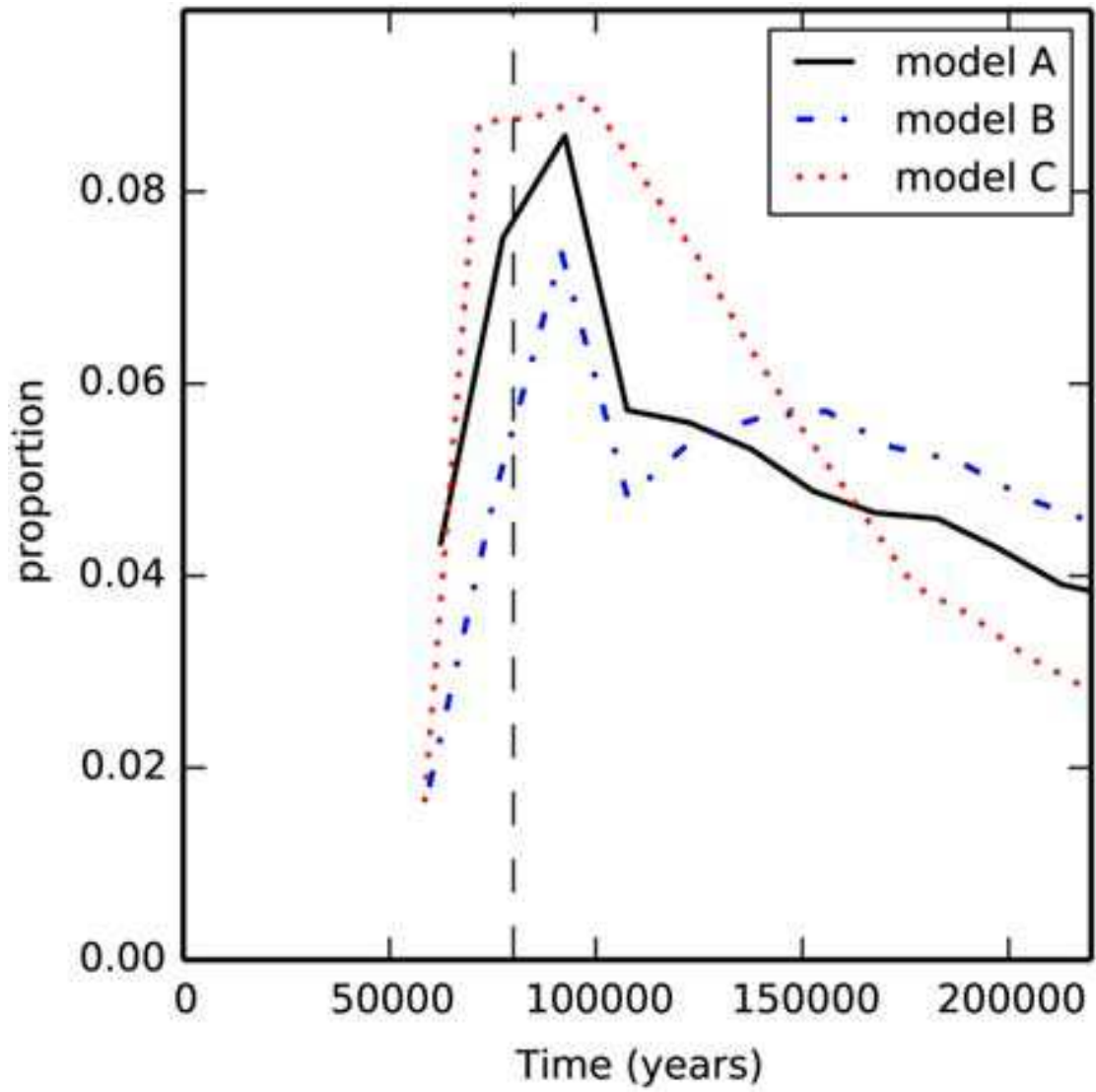


Figure 2 (in box 1). Distribution of the age of the L3 node in 20,000 simulations for each of the models listed in Table 2.

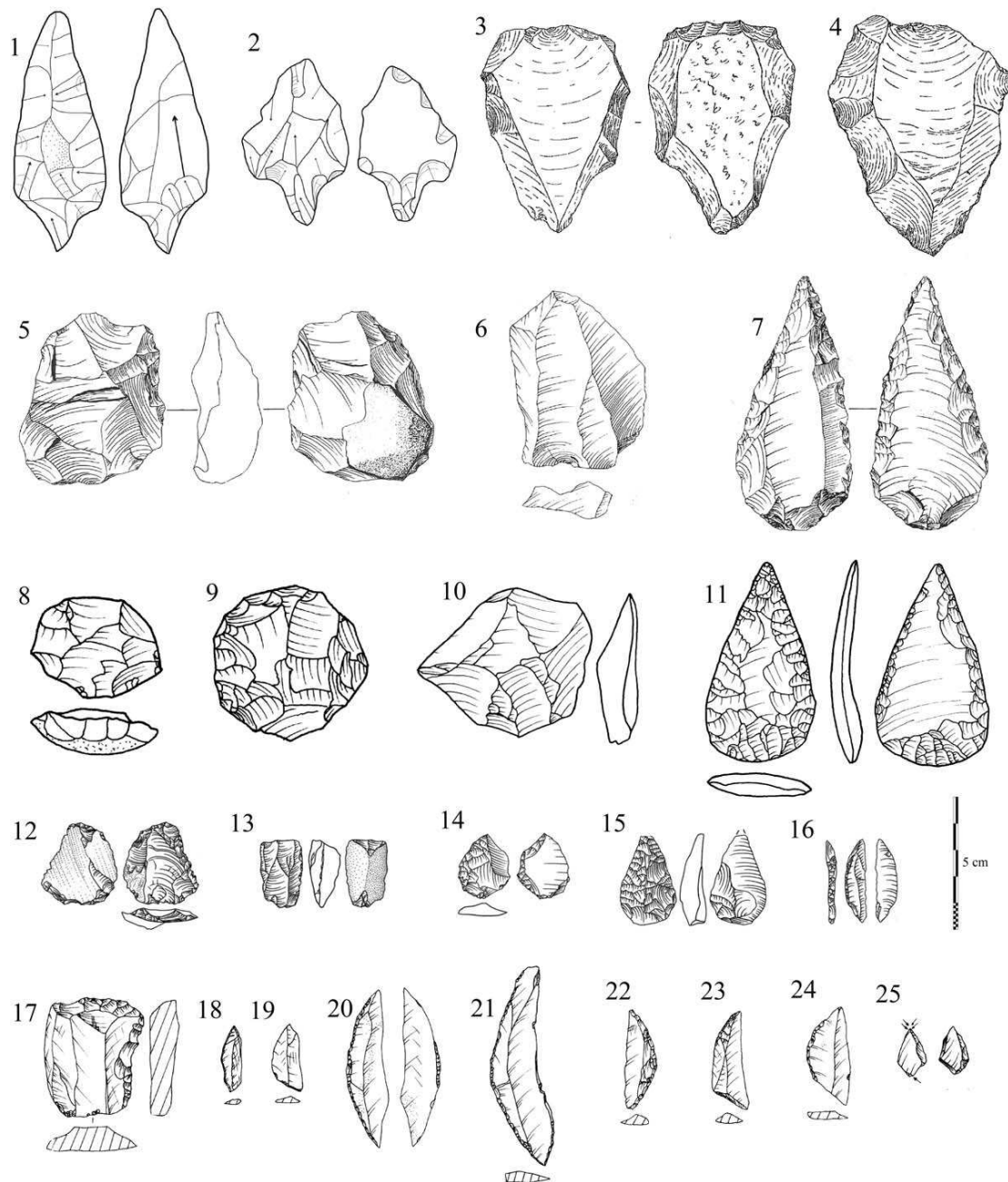


Figure 3. Selected lithics (stone tools) from East and North Africa for MIS 5 (1-11) and MIS 3 (12-25). 1-4: iconic MIS 5 Middle Paleolithic (Middle Stone Age) lithic types and techniques of North Africa, 1-2: tanged/pedunculated Aterian points, widely believed to have been hafted tools,⁶⁸ 3, 4: 'beaked' ('Nubian') Levallois cores,⁶² 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/microliths, 25: burin.¹⁰³

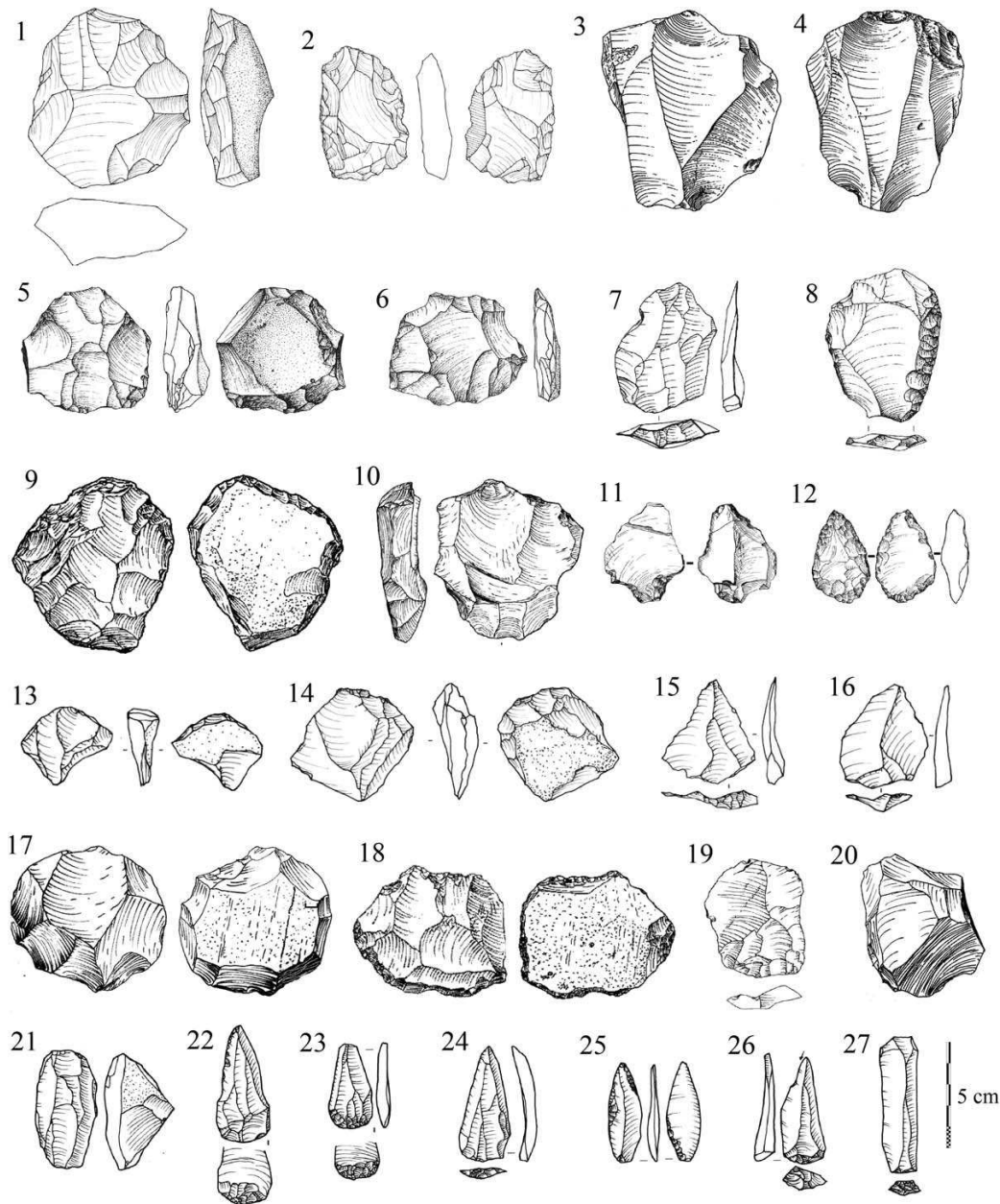


Figure 4. Selected lithics from Southwest and South Asia from MIS 5 (1-12) and MIS 3 (13-27). 1-4: Arabian Peninsula. 1: centripetally prepared preferential Levallois core, Jebel Faya, UAE, ~125 ka, 2: bifacially flaked tool, Jebel Faya,¹⁰⁴ 3,4: beaked (or Nubian) Levallois cores from TH-59, Oman, probably MIS 5,²⁰ 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/pedunculated flake, 12: retouched point,⁶⁶ 13-16, typical artefacts 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

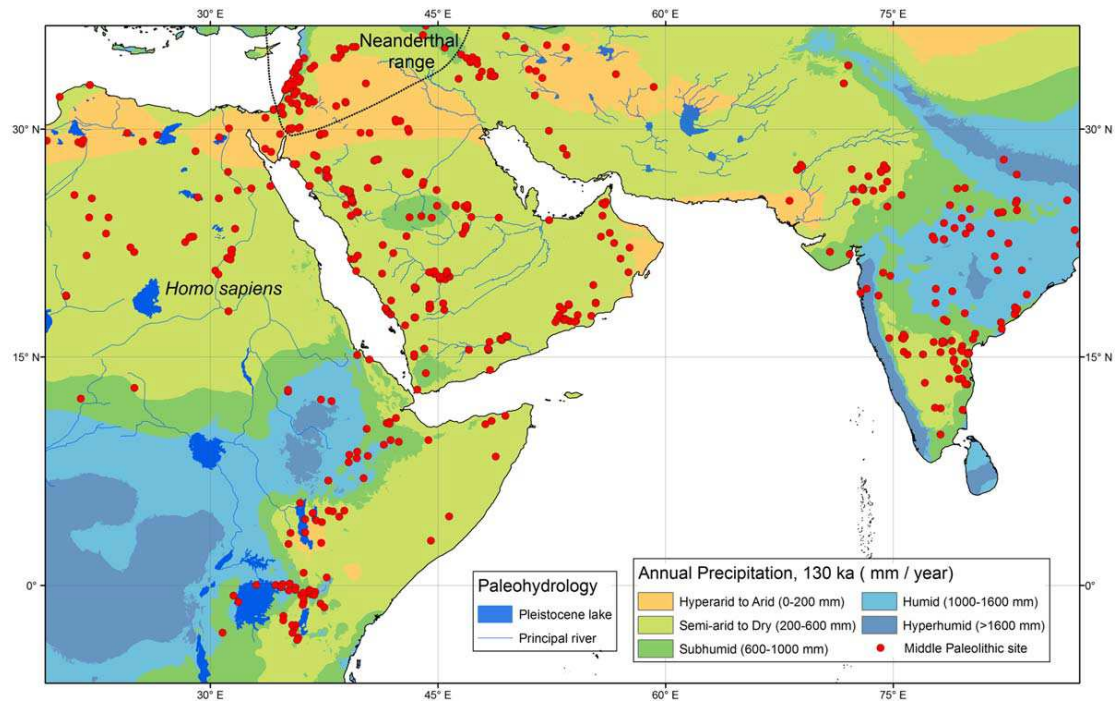


Figure 5. (in box 2) The distribution of Middle Paleolithic sites across East Africa, the Saharo-Arabian belt and India plotted on a modelled precipitation map for the last interglacial (MIS 5) with positions of major paleolakes (dark blue areas) and paleorivers which form extensive riparian corridors (blue lines). The dashed 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.

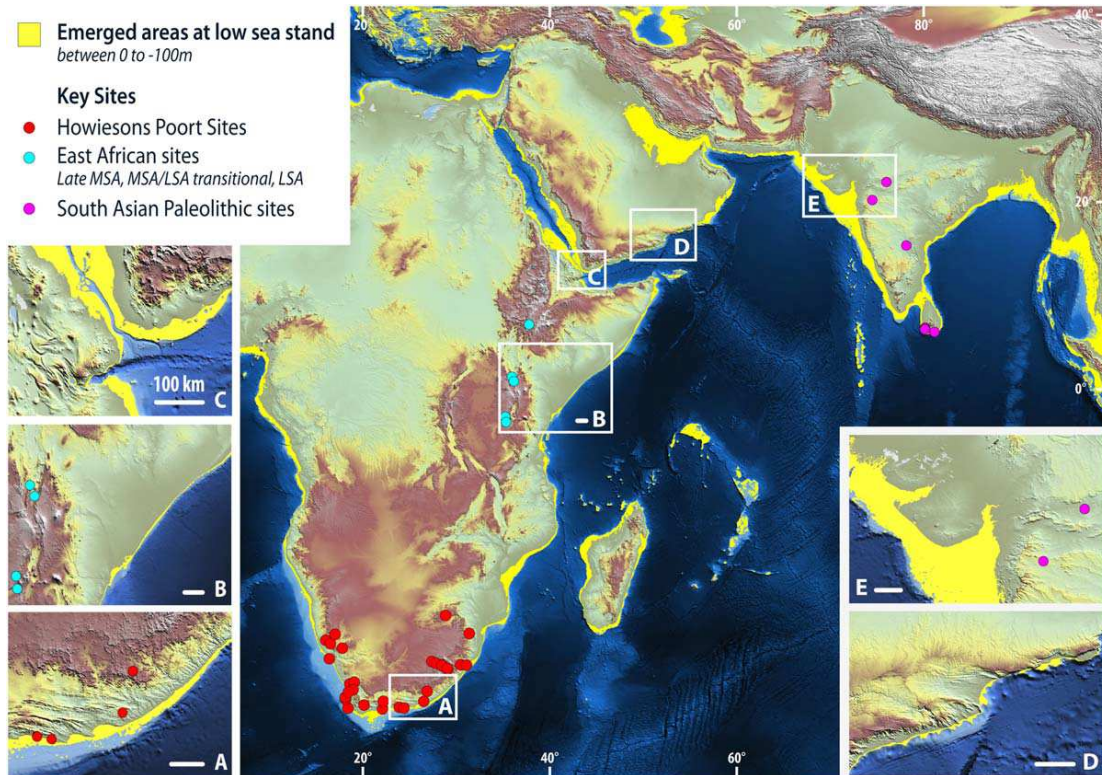


Figure 6. Map showing topography and bathymetry (SRTM30PLUS). Areas in yellow correspond to currently submerged land that would have been exposed when sea level was ~100m lower than present. Colored dots correspond to key archaeological sites (Howiesons Poort, MSA/LSA transitional and South Asian Late Paleolithic) emphasized by the Mellars *et al.* model.¹⁷ The inserts show that the landscape can be very different from place to place and that there is no ‘typical’ coastal environment.