REVIEW ARTICLE

Out of Africa: new hypotheses and evidence for the dispersal of *Homo sapiens* along the Indian Ocean rim

MICHAEL D. PETRAGLIA[1], MICHAEL HASLAM[1], DORIAN Q. FULLER[2], NICOLE BOIVIN[1] & CHRIS CLARKSON[3]

[1]*School of Archaeology, Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, UK,* [2]*Institute of Archaeology, University College London, London, UK, and* [3]*School of Social Science, University of Queensland, St Lucia, Queensland, Australia*

Abstract

The dispersal of *Homo sapiens* out of Africa is a significant topic in human evolutionary studies. Most investigators agree that our species arose in Africa and subsequently spread out to occupy much of Eurasia. Researchers have argued that populations expanded along the Indian Ocean rim at ca 60 000 years ago during a single rapid dispersal event, probably employing a coastal route towards Australasia. Archaeologists have been relatively silent about the movement and expansion of human populations in terrestrial environments along the Indian Ocean rim, although it is clear that *Homo sapiens* reached Australia by ca 45 000 years ago. Here, we synthesize and document current genetic and archaeological evidence from two major landmasses, the Arabian peninsula and the Indian subcontinent, regions that have been underplayed in the story of out of Africa dispersals. We suggest that modern humans were present in Arabia and South Asia earlier than currently believed, and probably coincident with the presence of *Homo sapiens* in the Levant between ca 130 and 70 000 years ago. We show that climatic and environmental fluctuations during the Late Pleistocene would have had significant demographic effects on Arabian and South Asian populations, though indigenous populations would have responded in different ways. Based on a review of the current genetic, archaeological and environmental data, we indicate that demographic patterns in Arabia and South Asia are more interesting and complex than surmised to date.

Keywords: *Dispersals, Homo sapiens, Indian Ocean, Arabia, South Asia*

Introduction

Questions about the origins of *Homo sapiens* and the spread of humans around the world fascinate scholars and the general public alike. In recent years, the broad outline of the

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Correspondence: Michael D. Petraglia, School of Archaeology, Research Laboratory for Archaeology and the History of Art, University of Oxford, Dyson Perrins Building, South Parks Road, Oxford OX1 3QY, UK. E-mail: michael.petraglia@rlaha.ox.ac.uk

biological and cultural evolution of our species has been documented through the efforts of scholars from a range of fields including biological anthropology, archaeology and population genetics. Available data from these disciplines points clearly to an emergence of *H. sapiens* in Africa. The earliest known fossils of *H. sapiens* are found in Africa, where they are recovered from contexts dating to ca 195–160 thousand years ago (ka) (White et al. 2003; McDougall et al. 2005) Based on mitochondrial DNA (mtDNA) gene tree analysis, the estimated time to the most recent common ancestor of all humans worldwide is ca 170 ka (Ingman et al. 2000). However, the ancestral relationships and demographic structure of *H. sapiens* populations remains complicated owing to considerable morphological variation in fossils (e.g. Gunz et al. 2009) and evidence from autosomal and X chromosome data suggesting that multiple archaic subpopulations contributed to the gene pool of early *H. sapiens* (Garrigan and Hammer 2006). The first secure evidence for the movement of *H. sapiens* outside Africa is recorded from the Levant, where modern human fossils and Middle Palaeolithic toolkits are found at ca 130–120 ka (Shea 2008). The extinction of *H. sapiens* in the Levant at 75–70 ka has been related to rapid climatic and environmental deterioration, which some tie to the Toba volcanic super-eruption of 74 ka and the subsequent onset of Oxygen Isotope Stage (OIS) 4 climatic cooling (Shea 2008).

Mitochondrial analyses indicate that populations of *H. sapiens* exited eastern Africa via southern Arabia (Quintana-Murci et al. 1999). Coalescence ages indicate that populations were present in South and Southeast Asia by ca 70–50 ka (Endicott et al. 2003, 2007; Metspalu et al. 2004; Macaulay et al. 2005; Thangaraj et al. 2005). Archaeological and fossil evidence meanwhile demonstrate that modern humans were present in Southeast Asia and Australia by ca 45 ka ago (O'Connell and Allen 2004; Barker et al. 2007). With respect to the northward spread of *H. sapiens* from Africa, archaeologists argue that modern humans were again present in the Levant at ca 45 ka, and spread from there to western Europe carrying Upper Palaeolithic technologies (Bar-Yosef 2007).

Based on genetic and archaeological data, researchers have recently argued that the dispersal of *H. sapiens* along the southern route would have involved a single, rapid population movement along coastlines (Macaulay et al. 2005; Bulbeck 2007). In a summation of the evidence, Mellars (2006a) claimed that the southern dispersal route was firmly established at 60 ka ago and that this event was marked by cresentic blade and microblade industries and symbolic traits associated with modern human behaviour. Mellars linked cresentic tool forms found in Sri Lanka and India to African industries, such as Howieson's Poort, and furthermore, observed similarities in engraved pieces found at Blombos, South Africa, to those of Patne in India. To Mellars, this strongly indicated a direct connection between early human colonists in Asia and their ancestors in Africa. The dispersal of *H. sapiens* out of Africa 60 ka ago, more than ca 100 ka after the estimated time to the most recent common ancestor, has raised questions about the development of cognitive, adaptive, and behavioural abilities of earlier African populations and why it took them so long to colonize areas outside of Africa (Mellars 2006b).

Problems with the consensus view of the southern dispersal

Although a broad consensus has formed concerning the dispersal of *H. sapiens* out of Africa, a number of problems pervade current interpretation. Discussions about modern human dispersal out of Africa have to rely on very limited fossil finds, such as those found in small areas of the Levant (Shea 2001). The Levantine record, which appears to show an extinction of *H. sapiens* at ca 75 ka, and a second advance at ca 45 ka, is clearly a limited, and geographically biased window on the dispersal of humans across Eurasia. For the southern

route via the Indian Ocean rim, the most serious problem for interpretation of dispersal processes continues to be the poor fossil evidence and the lack of high resolution, multidisciplinary archaeological research. Thus, most palaeoanthropological formulations concerning the southern route have been entirely theoretical, drawn from evaluation of fossil and archaeological evidence at either end of the dispersal route, in the Levant and Australasia. The fossil evidence for *H. sapiens* and their predecessors in most geographic areas along the Indian Ocean rim is virtually non-existent.

MtDNA and Y chromosome analyses repeatedly highlight the importance of the southern route; however, such analyses often assume that modern sampled populations are an accurate reflection of all past populations. Such studies rarely consider the effects of major demographic changes (population expansions, contractions and extinctions) resulting from climatic fluctuations in the Late Pleistocene, as well as from potential Holocene processes of farmer spread (e.g. Bellwood 2005). Since genetic studies centre on modern populations, coalescence ages measure reproductively successful lineages rather than providing a history of all lineages that may have been present. It nonetheless needs to be borne in mind that forager populations that once thrived in certain areas, such as deserts (e.g. the Empty Quarter of Arabia, or the Thar Desert of the Indian subcontinent), may have become extinct, so that their gene pools are no longer available for sampling in contemporary populations. Moreover, mtDNA mutation rate estimates suffer from calibration shortcomings, leading to widely disparate ages for estimating the timing of the southern dispersal (Endicott et al. 2009; Soares et al. 2009).

Recognizing these geographic biases and limitations, various researchers have sought to undertake more detailed and systematic studies in the overlooked but geographically critical regions of the Indian Ocean rim (e.g. papers in Petraglia and Allchin 2007; Petraglia and Rose 2009). Archaeologists, in particular, have begun to make substantive headway in synthesizing existing data and in conducting new field investigations in Arabia and South Asia, as summarized below. While dating of archaeological sites, excavation of stratified archaeological deposits, and detailed stone tool analyses and inter-site comparisons continue to be more limited than is ideal, recent findings arising from current archaeological investigations, together with new genetic research, are providing fresh, if tentative, insights into dispersal processes.

This article considers the occupation history of human populations in Arabia and South Asia in the Late Pleistocene. We introduce the genetic and archaeological data from each region, followed by a discussion of the implications of the evidence. We suggest the possibility that *H. sapiens*, using Middle Palaeolithic technology, dispersed from an African source in OIS 5. We argue that mtDNA and Y chromosome data drawn from contemporary populations record the most demographically successful lineages that survived Late Pleistocene environmental fluctuations, and are thus only a partial record of the dispersal of *H. sapiens* populations out of Africa. Based on synthesis of available genetic and archaeological data, and incorporation of new findings, we offer an alternative perspective on the southern dispersal, and suggest that the story of human movements out of Africa was probably more complex, and more interesting, than has previously been proposed.

Population history of the Arabian peninsula

Genetic studies

Genetic analyses indicate that early *H. sapiens* populations dispersing out of Africa passed eastwards into the Arabian peninsula via the Horn of Africa (Quintana-Murci et al. 1999).

The phylogenetic distribution of haplogroup M supports the notion that there was an early population exodus from Africa (Maca-Meyer et al. 2001). As the founder ages of M and N are similar, it has been hypothesized that both lineages were carried during the dispersal of humans out of Africa (Forster et al. 2001). In this view, the southern coastal route was the main corridor for population expansion, followed by a west Eurasian dispersal derived from a radiation from India (Oppenheimer 2003; Macaulay et al. 2005).

Genetic studies targeting populations in the Arabian peninsula have become increasingly contradictory in recent years, with some analyses now indicating only a minor African contribution to current gene pools (e.g. Kivisild et al. 2004; Abu-Amero et al. 2007; Alshamali et al. 2009). Others have indicated that M1 does not mark a southern dispersal but a backflow to Africa by Asian or Levantine carriers (Maca-Meyer et al. 2001; Olivieri et al. 2006; González et al. 2007). Complicating previous interpretations, the historic slave trade and demographic inputs during the Neolithic have also been implicated as major contributors to the presence of African and Near Eastern genes in Arabian populations (Luis et al. 2004; Abu-Amero et al. 2007; Rídl et al. 2009). As a consequence, mtDNA haplogroup data now shows decreasing support for the notion that Arabia was a demographic expansion centre in the Late Pleistocene; instead, the region is now viewed as a partial record and a recipient of multiple prehistoric and historic dispersals from Africa, India, Indonesia and Australia over the course of the Late Pleistocene and Holocene (Cerny et al. 2008; Abu-Amero et al. 2008). Some geneticists maintain that the Horn of Africa retains a genetic record indicative of the location having been a major intercontinental thoroughfare in an early 'Upper Palaeolithic' dispersal episode, although the Levantine corridor is considered the main African-Asian route for prehistoric gene flow from the Last Glacial Maximum (LGM) onwards (Rowland et al. 2007). Based on Y-STR diversity, other geneticists argue that the Arabian genetic data reflects a mosaic pattern that challenges interpretation of more global processes. Different regions appear to have been shaped by distinctive geographic and historical processes, with, for example, populations in the Gulf sharing more historical affinity with Near Eastern populations, and those in Saudi Arabia and Yemen having a relatively distinctive genetic background, perhaps due to isolation in desert environments (Alshamali et al. 2009).

The Middle Palaeolithic record

Archaeological surveys conducted across the Arabian peninsula indicate that Middle Palaeolithic sites are relatively numerous, and can be readily identified based on stone tool typology (Petraglia and Alsharekh 2003). Middle Palaeolithic core reduction methods have been described as plain flake, discoidal, Levallois, and blade. The great majority of Middle Palaeolithic sites in Saudi Arabia consist of plain flake cores and unifacially retouched tools on flakes. The high incidence of stylistically irregular and unstandardized flaking techniques in Saudi Arabia may be a product of raw material quality, as the available raw materials in many geographic regions are quartzite and ferruginous sandstone. Levallois cores have been identified, though the frequency of Levallois elements in assemblages is often noted to be generally low, particularly in Saudi Arabia. Some of the best and most frequent examples of Levallois cores have been found in the Hadramawt of Yemen, where centripetal, recurrent and convergent flaking patterns have been identified (Inizan and Ortlieb 1987; Cleuziou et al. 1992; Inizan et al. 1998; Crassard 2009).

In the Wadi Surdud of Yemen, near the Red Sea, stratified Middle Palaeolithic assemblages with Levallois assemblages have been excavated and dated to between 80 and 70 ka (Delagnes et al. 2008; Macchiarelli 2008) (Figure 1). In the case of the Yemeni sites, it
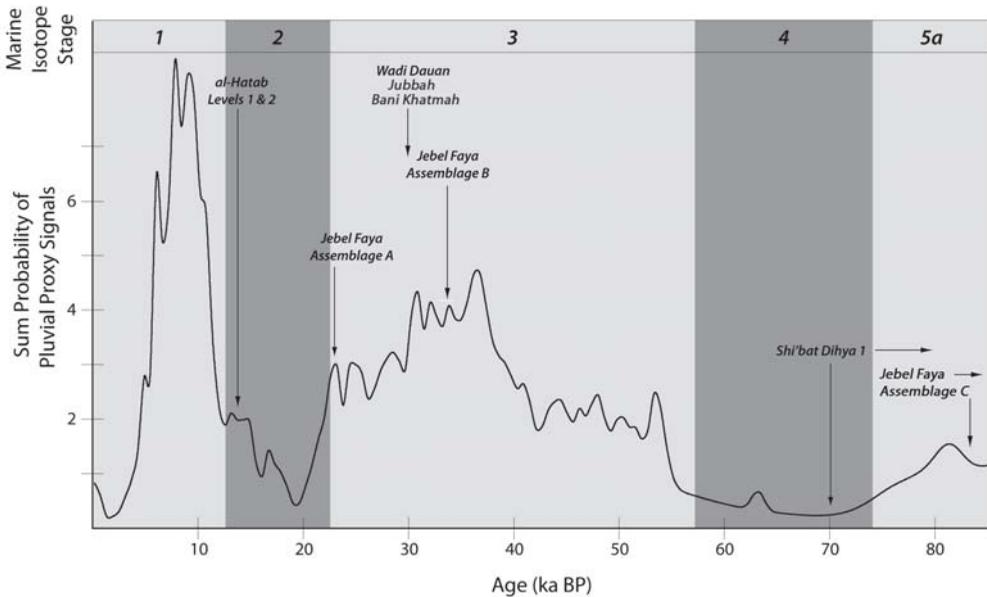
Figure 1. Marine Isotope Stages and recent chronometric ages for Middle Palaeolithic industries in the Arabian peninsula. Ages of archaeological sites: Jebel Faya (Marks 2009), Shi'bat Dihya 1 (Delagnes et al. 2008; Macchiarelli 2008), Wadi Dauan (Amirkhanov 1994), Jubbah (Garrard et al. 1981), Bani Khatmah (McClure 1994), al Hatab (Rose and Usik 2009). Marine Isotope graphic after Parker and Rose (2008).

appears that flint was readily available, allowing the manufacturers to produce predictable flaking outcomes. Excavations at the Jebel Faya 1 rockshelter in the UAE have produced stratified Middle Palaeolithic assemblages dating to OIS 5 and 3. One of the lowermost strata at Jebel Faya (Assemblage C) has yielded an age of > 85 ka, indicating a hominin presence in OIS 5a, and probably earlier given lower-lying stone tool assemblages. Assemblage C consists of cordiform handaxes, foliates, Levallois and discoidal cores, and a variety of retouched tools such as scrapers and denticulates (Marks 2009). In southern Saudi Arabia, the Bani Khatmah site situated near Late Pleistocene lakes yielded tanged points considered to be reminiscent of 'Aterian' assemblages of Africa (McClure 1994).

A number of Middle Palaeolithic sites have been identified along the Red Sea coastal plain (Zarins et al. 1980, 1981; Whalen et al. 1981, 1988), supporting the notion that dispersing populations used coastal routes (Petraglia and Alsharekh 2003). At several localities, Levallois flakes, blades, cores, and other tool types produced from the local lavas were recovered. Artefacts were situated at +2 m above mean sea level and ca 75 m from the Red Sea. In at least one case, the tools were reportedly firmly embedded in a coralline beach terrace (Zarins et al. 1980, 1981), though this has not been supported by recent observations (Bailey 2009). Middle Palaeolithic sites occur in potential crossing zones from Africa to Arabia, as 25 sites have been located in Yemen, near the Bab al-Mandab Strait (Whalen and Pease 1992). In addition to the sites situated along the Red Sea zone, Middle Palaeolithic occurrences have been identified along the Arabian Sea margin (Amirkhanov 1994; Petraglia 2007). However, there is as yet no convincing evidence of Arabian Middle Palaeolithic marine adaptations (Bailey 2009), and indeed undisputed evidence for maritime adaptation does not occur in the region until the mid-Holocene (Boivin et al. 2009).

Middle Palaeolithic sites have also been found in interior zones, situated along palaeo-rivers, streams and lakes (e.g. Parr et al. 1978; McClure 1976, 1978; Zarins et al.

1980, 1981). Surveys along extinct stream systems in the Hadramawt-Jawf region of Yemen have identified the presence of numerous Middle Palaeolithic sites (Inizan and Ortlieb 1987; Cleuziou et al. 1992). The Wadi Surdud assemblages of Yemen appear to straddle OIS 5a and OIS 4, as supported by the presence of grassland environments (based on presence of equids and bovids) and hyperarid conditions noted by isotopic and palaeobotanical evidence (Delagnes et al. 2008). The Jubbah Basin provides one of the best cases to support the presence of Middle Palaeolithic sites in the interior, along palaeolake margins (Garrard et al. 1981). Seven major sedimentary units were identified in 26 m of deposits, indicating fluctuations from stillwater phases to arid and aeolian conditions in the Holocene and Late Pleistocene (upper deposits yielded radiocarbon ages of ca 30 ka). Overlooking the palaeolake, two surface sites with Levallois elements were identified on elevated sandstone outcrops.

Implications of the Arabian evidence

The distribution of archaeological sites in the Arabian peninsula demonstrates that Middle Palaeolithic hominins expanded into new territories after their initial movements out of either Africa or the Levant. Though there are currently no known hominin fossils in Arabia, the nearby finds of *H. sapiens* from Skhul and Qafzeh in the Levant are instructive and suggest that early populations of humans could have penetrated Arabia between 130 and 75 ka ago, perhaps followed by later population spreads by ca 60–50 ka ago. Such a scenario would be consistent with mammalian data, which indicates a movement of fauna into Arabia from Africa in the Late Pleistocene (Delany 1989) and mtDNA studies of the Hamadryas baboon which indicate multiple phases of range expansion from Africa, including at ca 330 ka, 220 ka, 120–110 ka and 80 ka (Fernandes 2009).

Mitochondrial and Y chromosome data extracted from contemporary human populations do not necessarily yield information reflective of the earliest exits of populations of *H. sapiens* out of Africa. Indeed, interpretation of the original dispersal of humans into Arabia from a genetic perspective has become more rather than less complicated in recent years, owing to improvements in the sampling of regional populations. This has led to the realization that the modern gene pool of Arabia is the consequence of a series of separate demographic events over a long time period, including probable loss and contraction of populations as a result of severe aridity events, and Neolithic and historic population expansions, interactions and movements. Nevertheless, mtDNA evidence does suggest the possibility that populations carrying L3 may have entered into Eurasia and Arabia at an early date, corresponding with favourable environmental conditions at ca 100–80 ka (Cabrera et al. 2009). Since coalescence dates for haplogroup M average between ca 73–55 ka, there is a possibility that M lineages may have been present in Arabia and in regions to the east by this time. In this view, the return of arid conditions in OIS 4 would have affected the descendants of the L3 carriers, resulting in bottlenecks and loss of lineages (Cabrera et al. 2009). Populations that survived OIS 4 conditions would have been the direct ancestors of all present day M and N branches. If this is the case, then it is not necessary to invoke a rapid southern dispersal to explain the near-simultaneous existence of populations as distant as South Asia to Southeast Asia.

In the absence of detailed technological comparison, it remains difficult to conclusively support Arabian connections with the African Middle Stone Age (MSA) or the Levantine Mousterian. It is conceivable that some Middle Palaeolithic industries, particularly in northern Arabia, were produced by Neanderthals, though Arabian landscapes are unlike the geographic ranges normally inhabited by these hominins (Churchill 1998). Arabian Middle Palaeolithic assemblages in the Hadramawt of Yemen are said to resemble the

Levantine Mousterian (Crassard 2009). This argument is supported by archaeological investigations at the Wadi Surdud in Yemen, which show that 80–70 ka lithic assemblages are similar to those in the Levant (Delagnes et al. 2008; Macchiarelli 2008). Such an age range would correspond with the presence of *H. sapiens* in the Levant, though it is at the margin of the Neandertal re-expansion. Certain researchers have pointed out that Arabian assemblages are similar to those produced by *H. sapiens* in the African MSA (Beyin 2006). This includes evidence that there was a late Aterian presence in southern Saudi Arabia (McClure 1994), that foliate point styles are similar between Sudan and Oman (Rose 2004a, 2004b), and that a Nubian core technology is present in the Jebel Barakah assemblages of the UAE (Wahida et al. 2009). The Jebel Faya assemblages in the UAE, dating to > 85 ka, share similarities with stone tool assemblages in East and Northeast Africa, particularly those associated with the Late Sangoan (Marks 2009).

Assemblages situated at the extreme southern and eastern margins of Arabia do not seem to share clear technological parallels with those in central Saudi Arabia. Archaeologists describing Middle Palaeolithic sites in Saudi Arabia repeatedly note that Levallois core technology is under-represented in comparison with the Levantine Mousterian. Whalen and others (1981) stressed that core reduction and flake preparation methods in Arabia may have followed their own technological trajectory, comprising a distinct stylistic tradition and representing a specific adaptation to local environmental conditions, a point also made for the younger assemblages at Jebel Faya (Marks 2009). Indeed, many of the technologies found in central Saudi Arabia involve unstandardized and discoidal reduction that does not clearly resemble that found in the Levant. Such observations are difficult to interpret, but technological and stylistic similarities with both the Levant and Africa in part reflect the fact that there were different source areas for Arabian populations at different times. While the similarity of technologies in Africa and southern Saudi Arabia, Oman and the Gulf are easier to reconcile from the perspective of dispersal processes, it is more difficult to understand how the Yemeni assemblages relate to the Levantine Mousterian. The Hadramawt and Wadi Surdud assemblages of Yemen do not share clear technological parallels with large parts of Saudi Arabia, which separates Yemen from the Levant. As a consequence, this must mean that either similar technologies remain currently unidentified in Saudi Arabia, the Yemeni assemblages have been misinterpreted as to source area, or the Yemeni finds are the result of technological convergence.

With respect to entry points into Arabia, it is difficult to provide definitive evidence, and indeed it is probable that populations at different times would have used different corridors as they emerged out of Africa. If the initial dispersal source emanated from the Sinai or Levant, it would seem likely that populations moved southwards along the Red Sea, eventually passing along the Arabian Sea. However, if the Bab al-Mandab Strait was a crossing zone, populations would have likely expanded in two directions, northwards along the Red Sea and eastwards along the Arabian Sea. The presence of Middle Palaeolithic sites near the Bab al-Mandab is suggestive of a crossing from the Horn of Africa. The Red Sea featured shallow sea levels during OIS 6, ca 135 ka (Rohling et al. 1998), increasing the ease of passage for populations across the Bab al-Mandab, either through an overland connection or across a reduced waterway. Of course, it is possible that humans crossed the Strait at other times, and if early humans employed watercraft of some form, then such waterways could have provided relatively easy passage. If separate African populations travelled along two corridors (i.e. North Africa, Horn of Africa) as they emerged from Africa, cultural and biological exchanges would have taken place in Arabia, particularly along the Red Sea zone.

Once present in Arabia, site distributions clearly show that Middle Palaeolithic populations expanded into interior zones along river valleys. Mapping of sites in the Hadramawt

indicates that populations moved up the riverine landscapes of the Jawf system, penetrating many zones and eventually reaching the headwaters of rivers located in mountainous regions that would have been more heavily vegetated. During climatic ameliorations, populations probably expanded into the interior of the Arabian peninsula, settling along rivers and lakes in inland areas. Some zones contain concentrations of sites, dense artefact accumulations numbering into the thousands, and artefact scatters ranging over 12 500 m^2 (e.g. Gilmore et al. 1982; Whalen and Pease 1992). Hominins dependent on fresh water sources for survival would have been challenged by increasing aridity, as clearly documented at several points in the Late Pleistocene (e.g. Glennie and Singhvi 2002; Fleitmann and Matter 2009; Preusser 2009). Moderately dry phases would have led to significant changes in local ecological conditions, requiring hominins to make adaptive adjustments. The diversity of stone tool assemblages, employing a variety of reduction strategies, may be a sign of flexible responses to local ecological change. More severe changes, including the drying of lakes, would have driven populations to refugia where springs remained active along the Red Sea, the Arabian Sea and the Gulf (Marks 2009; Rose and Petraglia 2009), though it is also possible that some local populations were driven to extinction. The relative abundance of Middle Palaeolithic sites in Arabia indicate that populations were either able to persist through moderate climatic changes or to re-advance after the conclusion of the most arid periods. Such contractions and depopulation events across large expanses of the desert zones of Arabia mean that demographic interpretations involving DNA drawn from modern Arab populations should be treated with caution.

Population history of the Indian subcontinent

Genetics

Phylogenetic patterns from both mtDNA and the Y chromosome data support the colonization of South Asia by *H. sapiens* who originated in Africa (Kivisild et al. 1999, 2003; Metspalu et al. 2004; Trivedi et al. 2008). South Asian lineages belong to mtDNA haplogroups M and N (groups U and R being major subclades of N), which are descended from the L3 haplogroup (Kivisild et al. 1999; Macaulay et al. 2005; Torroni et al. 2006). The coalescence dates for haplogroup M (specifically U2i, M2, R5) in South Asia average between 73 and 55 ka, and may represent an India-specific subclade related to the original dispersal event into the subcontinent (Kivisild et al. 2000). These early coalescence dates are supported by those obtained from the Andamanese M31 and M32 and Malaysian M21 and M22 lineages (Macaulay et al. 2005; Thangaraj et al. 2005). The geographic origin of the M lineages remain uncertain, and as indicated above, include suggestions for a Southwest Asian origin (e.g. Richards et al. 2003; Roychoudhury et al. 2001). There are arguments for an African origin for the M1 lineage (Metspalu et al. 2004) as well as arguments for a backflow to Africa (Maca-Meyer et al. 2001; Olivieri et al. 2006; González et al. 2007). Re-evaluation of the mtDNA evidence raises the possibility that L3 populations dispersed from Africa, reaching geographic areas along the Indian Ocean rim by 100-80 ka (Cabrera et al. 2009).

Whatever the timing of the dispersal of *H. sapiens* into the subcontinent, the route or routes out of Africa remain controversial (Forster and Matsumura 2005). The great time depths apparent in the Andamanese and Malaysian mtDNA have been argued to support the rapid colonization of the region as part of a southern coastal route to Australia (Endicott et al. 2003; Macaulay et al. 2005; Thangaraj et al. 2005). Genetic research continues to document population dispersals from the Indian subcontinent towards Southeast Asia and

Australasia (Roychoudhury et al. 2000; Majumder 2001; Kumar et al. 2009). Proponents of the southern dispersal route have argued for a rapid initial dispersal around the South Asian coastline (e.g. Oppenheimer 2003, 2009), but some geneticists argue that the mtDNA evidence simply suggests expansions of *H. sapiens* populations within South Asia close to its initial colonization (Kivisild et al. 1999; Metspalu et al. 2004; Atkinson et al. 2008).

Though the distribution of haplogroup M has been used to support the southern dispersal model, the coalescence age of haplogroup M in India (ca 45 ka) is considerably younger than in East Asia (ca 65 ka), which does not make sense if India was part of the original route of population movements. This has suggested to some a backward movement of populations into South Asia after the Toba super-eruption of 74 ka ago, as a consequence of a bottleneck and re-expansion (Oppenheimer 2003, 2009). Moreover, there have been suggestions that there was a backward migration to India from the Andaman Islands as well as post LGM migrations to the islands from Southeast Asia (Barik et al. 2008). Alternatively, an explanation of this young coalescence age is that after initial human settlement, the demographic history of the Indian subcontinent was staggered by several indigenous Late Pleistocene expansion events around 30 ka (Sun et al. 2006), a scenario earlier proposed based on mtDNA hypervariable region analyses (Kivisild et al. 1999), and now confirmed through examination of M coalescence estimates using synonymous substitutions (Petraglia et al. 2009a).

Hominin fossils

Hominin fossils relevant to the initial human colonization of the Indian subcontinent have not been recovered. The only known pre-modern fossil in South Asia was recovered from the central Narmada river valley, at Hathnora (Sonakia 1985). The taxonomic status of the calvarium is still disputed, as it was originally classified as *Homo erectus* by its discoverer, and later identified as 'archaic *Homo sapiens*' (Kennedy 2000). Re-evaluation of the calvarium indicates shared morphological traits with *Homo heidelbergensis* and *H. erectus*, though it may be best classified as an indeterminate form of *Homo* (Athreya 2007). Geological, palaeontological and archaeological data suggest a late Middle Pleistocene association of the fossil (Kennedy 2000), with an age of 236 ka (Cameron et al. 2004), though recent research indicates a potential age of 160–85 ka (Patnaik et al. 2009). A key point here is that the archaic hominin is associated with Late Acheulean artefacts.

Though fossils of *H. sapiens* have been reported from the Indian subcontinent, their precise chronometric ages remain uncertain (Kennedy 2000). The most secure fossils identified as *H. sapiens* are in Sri Lanka, where partial skeletons have uncalibrated radiocarbon ages of ca 31 ka in Fa Hien Cave and 28.5 ka at Batadomba-lena Cave (Deraniyagala 1992). This is supported by the recovery of fragmentary *H. sapiens* skeletal evidence in the Jwalapuram Locality 9 rockshelter in southern India, dating to 17–10 ka (uncalibrated) (Clarkson et al. 2009). There is clearly currently a wide chronological gap between the archaic Narmada hominin and the fossils of *H. sapiens* that date to the latter part of the Late Pleistocene.

The Middle Palaeolithic record

The distinction between Late Acheulean and Middle Palaeolithic tool assemblages in South Asia is sometimes difficult to identify as typological and technological changes are gradual over the transition (Misra 1985; Petraglia et al. 2003; James and Petraglia 2009). Nevertheless, Late Acheulean assemblages are marked by the presence of diminutive bifaces

(including handaxes and cleavers) and flake tools produced from prepared cores. Late Acheulean sites are relatively young, ranging up to 120–100 ka (Sharma and Clark 1983).

The Middle Palaeolithic of the subcontinent is abundant, with the number of identified sites ranging into the many hundreds. Surveys in river valleys have identified large numbers of Middle Palaeolithic sites (e.g. 115 in the Ghataprabha Basin, 80 in the Malaprabha Basin) (Pappu and Deo 1994). Concentrations of Middle Palaeolithic sites along rivers and in basins indicates that hominin populations were present in attractive zones over a relatively long time interval (Korisettar 2007).

Middle Palaeolithic core reduction methods are diverse and include plain flake, discoidal, Levallois, and blade techniques (Jayaswal 1978; James and Petraglia 2005). Though these reduction methods were widely used, the frequency of their occurrence appears to vary across the subcontinent (James 2007, 2009). Levallois and discoidal techniques are the most commonly identified core preparation techniques, but unprepared and cylindrical methods (e.g. Misra 1967, 1968; Jayaswal 1978) and blade and flake-blade components have also been reported (e.g. Misra 1985, 1989, 2001; Allchin et al. 1978). The best studied Middle Palaeolithic assemblages have been recovered in deposits from the southern Indian Jurerru Valley dating to between 78 and 38 ka (Petraglia et al. 2007, 2009b). A variety of core types were recovered, including multiplatform, single platform, unidirectional, and Levallois types. Retouch is characteristically informal and unstandardized, with atypical scrapers and notched flakes forming the majority of retouched tools.

Stone tool assemblages show increasing diversity from about 45 ka ago, characterized by the production of sites with a notable blade component. This transitional phase is traditionally classified as the 'Upper Palaeolithic' of South Asia, and typically divided into Flake-Blade, Blade-Based and Blade and Burin Industries (Murty 1979). The so-called Upper Palaeolithic industries are not as common as Middle Palaeolithic industries and they appear to be variable in core reduction methods and tool types, though there is a general increase in the production of burins and backed tools at some sites (Murty 1979; Paddayya 1984). South Asian microlithic industries, often referred to as 'Mesolithic', date to at least 29.4 ka in India and 28.5 ka in Sri Lanka (uncalibrated) (Deraniyagala 1992; Clarkson et al. 2009; Petraglia et al. 2009a), indicating that they may be part of a diverse later Pleistocene package. At around 30 ka, there is contemporaneity between flake- and blade-based technology and microlithic industries, suggesting that a 'Late Palaeolithic' label may be more appropriate to characterize the unique character of the South Asian industries (James and Petraglia 2005).

Middle Palaeolithic sites are found in a variety of settings, such as in upland and lowland zones, open-air settings along perennial and seasonal streams, inter-dunal settings, and in rockshelters and caves. Middle Palaeolithic habitation in the Thar Desert zone was possible during periods when perennial water sources were present, though expansions of the desert during glacial periods would have made habitation more difficult (Misra 1995a,b). The presence of Middle Palaeolithic assemblages at ca 126–108 ka in the 16R dune of the Thar Desert corresponds with a high percentage of C4 plants and evidence for high summer rains and a strong monsoon with the OIS 5 interglacial (Achyuthan et al. 2007) (Figure 2). Recovery of Middle Palaeolithic assemblages in peninsular India dating to between 78 and 74 ka indicate that hominins were present during wetter environments of OIS 5a (Petraglia et al. 2007). Ages for Middle Palaeolithic assemblages between 74 and 38 ka indicate that hominins were present, and able to cope with more severe and fluctuating ecological conditions throughout OIS 4 and OIS 3 (Petraglia et al. 2007, 2009b). Note that, given the prevalence of Middle Palaeolithic sites in the region and the evidence for ecological flexibility, it is likely that the current lack of sites dated ca 100–80 ka results from a shortage
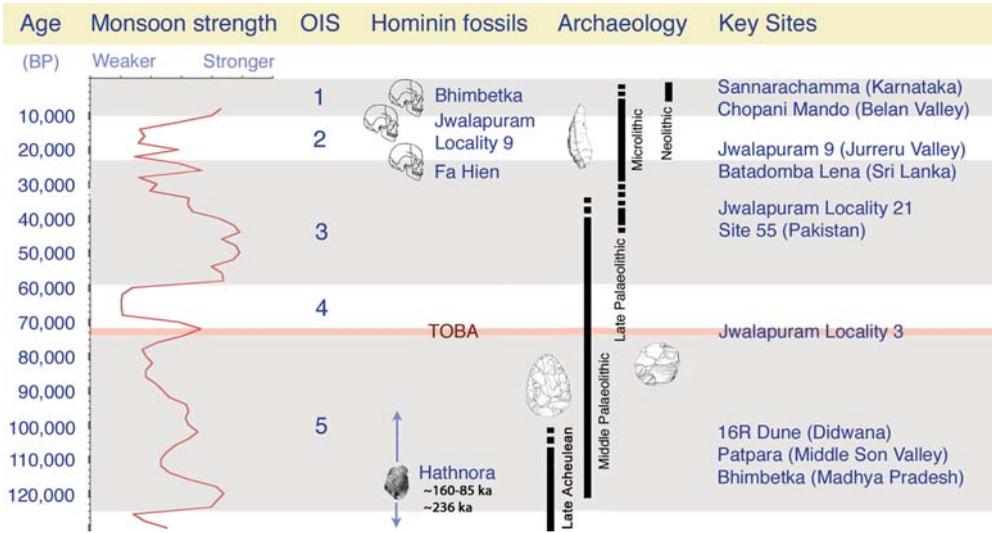
Figure 2. South Asian monsoon strength, hominin fossils and key archaeological sites and industries.

of reliable Late Pleistocene dating programmes in South Asia rather than an occupational hiatus. There are indications that even during the most severe climatic intervals in the Late Pleistocene, South Asia contained a mosaic of ecological settings, including woodlands, grasslands, tropical forests and deserts, allowing populations to persist and adapt to changing conditions (Petraglia et al. 2009a).

The evidence for the majority of the traits now commonly cited as evidence for modern human behaviour is relatively sparse in South Asia (James and Petraglia 2005; James 2007; Petraglia 2007). Though certain traits may extend as far back ago as the Acheulean, the clearest and most reliable evidence for symbolic thought and the construction of structures dates to ca 45 ka and younger. After 28.5 ka, a range of novel technologies are introduced, including the manufacture of bone tools and geometric microliths (Deraniyagala 1992; Clarkson et al. 2009). Even though the data is spatially and temporally sparse, Late Palaeolithic populations were clearly capable of explicitly symbolic behaviour, indicating that site occupants were behaviourally modern in their adaptations (James 2007; Petraglia 2007).

Implications of the South Asian evidence

The age range of 160–85 ka for the archaic hominin at Narmada is evidence for the survival of these hominins in OIS 5. The presence of Late Acheulean industries dating up to 100 ka probably relates to the presence of these archaic populations. Based on the identification of *H. sapiens* in the Levant between 130 and 75 ka, it is conceivable that the Indian Middle Palaeolithic assemblages correspond with an early expansion of *H. sapiens* from the west. Though Middle Palaeolithic assemblages have been dated to ca 128–108 ka in the 16R dune, it is unclear who produced this industry, and unfortunately these stone tool assemblages remain poorly described. The best dated and studied Middle Palaeolithic sites in India are the Jwalapuram assemblages, which range in age from 78 to 38 ka (Petraglia et al. 2007, 2009). Therefore, there is a hiatus between the Late Acheulean industries at 100 ka, and the Middle Palaeolithic assemblages dating to 78 ka, perhaps indicating that archaic hominins were extinct by the time of the arrival of *H. sapiens*. If, however, the Middle Palaeolithic

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industries from 16R (128–108 ka) are a sign of the presence of *H. sapiens*, it is possible that archaic and modern humans may have overlapped temporally.

The Middle Palaeolithic artefact assemblages dating to between 78 and 74 ka at Jwalapuram in peninsular India were suggested to be the product of *H. sapiens*, based in part upon their close technological similarity with MSA assemblages of Africa (Petraglia et al. 2007). However, such a date range for *H. sapiens* in the subcontinent does not correspond with genetic coalescence ages, which indicate a younger dispersal event, at ca 70–55 ka. This temporal disjuncture led to the suggestion that the Jwalapuram assemblages may mark the presence of earlier human populations for which there is no surviving genetic evidence (Endicott et al. 2009). Since lower confidence limits place *H. sapiens* in South Asia after 70 ka (Soares et al. 2009), the genetic evidence must signal that a colonization event occurred at about this time, or alternatively, later large-scale demographic growth may have masked the presence of earlier and smaller populations (Petraglia et al. 2009a). Since ancient DNA has not been recovered from South Asian skeletal collections, it remains unclear whether or not small forager populations have been demographically swamped by later population increase. Archaeological evidence suggests that Middle Palaeolithic hominins survived the fallout from the Toba super-eruption event of 74 ka ago (Petraglia et al. 2007). Though this evidence does not support a complete replacement event, it does not discount the possibility that some hominin groups were more affected by climatic and ecological changes than others, perhaps leading to the demise of some forager populations (Jones 2007). If this is the case, it is conceivable that the gene pool of the relatively small groups that survived Toba are no longer represented in modern sampled South Asians due to disappearance of some lineages and later demographic expansions (Sun et al. 2006; Atkinson et al. 2008; Petraglia et al. 2009a).

Modelling of OIS 4 environments and analysis of least cost topographic routes indicated that *H. sapiens* populations probably expanded along coastlines as they entered the subcontinent (Field et al. 2007), supporting the idea of a coastal model (Bulbeck 2007). However, only a few near-coastal and estuarine sites have been identified in the subcontinent (Marathe 1981; Rath et al. 1997) and none of these shows marine adaptations. If *H. sapiens* reached South Asia during OIS 5, when environments were most favourable, it is possible that interior zones, rather than coastal margins, were used as dispersal corridors (Figure 3)[1]. This lends support to Korisettar's (2007) suggestion that hominin populations would have found accessible transcontinental routes, travelling through the Himalayan passes and the interior basins of the peninsula. In this view, transcontinental routes and the wide distribution of river valleys and basins were more conducive than coastlines to human population movements owing to the presence of reliable freshwater resources (in the form of lakes, streams and springs), lithic resources and varied woodland and grassland eco-zones with a high concentration of animal communities. In this model, occupation in the geological basins was especially attractive during periods of heightened climatic aridity. Archaeological surveys in basins substantiate this claim as they contain a large number of Pleistocene sites (e.g. Sharma and Clark 1983; Pappu and Deo 1994).

In contrast to the 'human revolution' model, the archaeological record of South Asia shows no rapid or sudden appearance of a modern behavioural package as witnessed in western Europe; instead, the record has been characterized as temporally gradual in its assembly, and spatially patchy in the appearance of modern traits (James and Petraglia 2005). The clearest signature of the appearance of modern human behaviour occurs after 45 ka (well after the known presence of *H. sapiens* based on genetic data and archaeological and fossil findings from Australia), when the technological record shows a gradual shift in a more diversified technology and the rare introduction of traits considered to be part of the
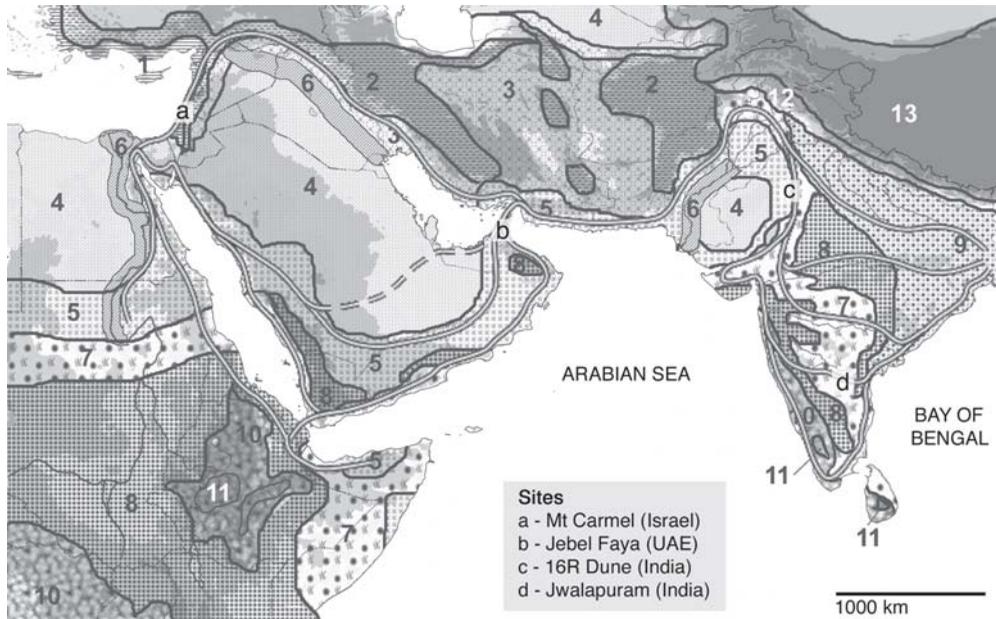
Figure 3. Reconstruction of OIS 5 environments along the Indian Ocean rim. Shown are hypothetical dispersal routes, with the location of key archaeological sites. The dashed line through central Arabia represents a route that takes into account the presence of palaeo-drainages (see Edgell 2006). Environmental key: 1, Mediterranean vegetation; 2, Mediterranean park-steppe (the classic 'fertile' crescent vegetation famous for wild cereal progenitors such as wheat and barley); 3, Dry steppe (of the middle East and southern Central Asia); 4, Desert; 5, Sub-Desert/ Sahel vegetation (generally of the Sudano-Sindhian floristic province); 6, Riverine corridors (marshes and gallery forests); 7, Tropical savanna/woodland-grass mosaic (including the tropical evergreen zones of India); 8, Dry tropical woodland (including dry deciduous zones of India); 9, Moist tropical woodland and grassland mosaic (in particular that of eastern India and Ganges plain in which Dipterocarpaceae including Shorea are frequent; this zone extends to Southeast Asia); 10, Moist tropical woodlands (including both Moist Deciduous zones like those in India and true tropical rainforests); 11, Tropical montane vegetation; 12, Warm temperate hill and sub-montane vegetation (including the vegetation of the Himalaya foothills); 13, High elevation coniferous forests and desert/ the Tibetan plateau.

modern human behavioural package (e.g. built structures). The most significant technological shift after the use of the long-lasting Middle Palaeolithic technology occurs at ca 35–30 ka ago (cal. BP), when microlithic industries develop across South Asia (Petraglia et al. 2009a). In this case, demographic growth and contractions in favourable ecological zones at this time may be responsible for stimulating the development of more efficient hunting technologies. Increasing levels of symbolism (i.e. beads, rockart) during arid phases of OIS 3 and 2 may have been the consequence of territoriality and increasing levels of population differentiation (Petraglia 2007; Clarkson et al. 2009).

Discussion: Dispersals along the Indian Ocean rim and the spread of *Homo sapiens* in perspective

Timing of dispersal

The archaeological evidence compiled here suggests that *H. sapiens* expanded out of Africa using Middle Palaeolithic technologies, supporting earlier theoretical arguments for a Mode 3 expansion event (Lahr and Foley 1994, 1998; Foley and Lahr 1997). Substantive

archaeological evidence in the form of dated Middle Palaeolithic technologies in the Arabia–South Asia transit zone now join early *H. sapiens* data from the Levant in supporting such an inference (Petraglia 2007) (Figure 4). This view contrasts with the notion that expansions of *H. sapiens* occurred at ca 50 ka, only after so-called modern cultural behaviours appeared (Klein 2000) or that population movements occurred at 60 ka based on a genetic coalescence age and the appearance of cresentic tool industries (Mellars 2006a).

We suggest that the first dispersal of *H. sapiens* along the Indian Ocean rim may be considerably earlier than currently realized. The evidence for a dispersal to the Levant by *H. sapiens* at 130–75 ka may not be evidence of a failed dispersal; rather, we suggest that the Levantine populations may be one example of successful OIS 5 range expansion across Arabia and South Asia (Figure 4). We base this inference on new ages from Middle Palaeolithic assemblages in Arabia (> 85 ka) and in India (78–74 ka), and their technological similarity to MSA assemblages in Africa. These chronometric ages are beyond the coalescence ages of 70–50 ka drawn from the modern human gene pool. If the earlier archaeological ages mark the presence of *H. sapiens* in Arabia and South Asia, it is clear that these populations are not being sampled in the remnant tribal groups of these regions. Of course, this argument makes much sense in Arabia, where OIS 4 and OIS 2 glacials resulted in spatially extensive desertification across the peninsula, almost certainly leading to significant population contractions or even extinctions.

The picture in South Asia is likely to be somewhat different, however. Arid phases in South Asia would have led to the expansion of the Thar Desert, but also the production of tropical forest refugia in southwest India and Sri Lanka, as well as the widespread creation of fragmented, mosaic grasslands and woodland habitats in most of the subcontinent. Small groups of foragers could have easily survived and pursued their hunting and gathering lifestyles in this range of habitats. Though some of these small groups of Middle Palaeolithic foragers survived the Toba super-eruption event of 74 ka, it is also possible that there were population-level impacts (Ambrose 1998; Jones 2007). We propose that these small South Asian populations are not represented in the modern gene pool due to demographic growth after ca 35 ka, leading to a massive population increase and replacement in the Middle and Late Holocene. If this scenario is accepted, it calls into question the accuracy of the view that populations first colonized the subcontinent at 60 ka. It is entirely possible that populations of *H. sapiens* were present in South Asia for a considerable period of time, and that they spread further eastwards at some point after 60 ka, eventually to occupy Australia before 45 ka, supported by recent genetic analysis of Indian and Australian populations (Kumar et al. 2009). This model of course puts emphasis on the need to recover hominin fossils, retrieve ancient hominin DNA and conduct systematic archaeological dating programmes.

Biogeography

Several important biogeographic implications emerge from the evidence that we have presented here. As indicated above, it is entirely conceivable that *H. sapiens* were present in Arabia in OIS 5, and perhaps as early as OIS 5e. If this is the case, Neanderthal re-occupation of the Levant at 75–47 ka may not signal the extinction of *H. sapiens* populations in Eurasia, as small groups may have been present in Arabian refugia. Once *H. sapiens* spread eastwards, they may have encountered Neanderthals in the upland belt of Iran and Pakistan (Finlayson and Carrión 2007: Figure 1); alternatively, *H. sapiens* populations may have avoided this already occupied zone by travelling along the non-mountainous littoral belt.
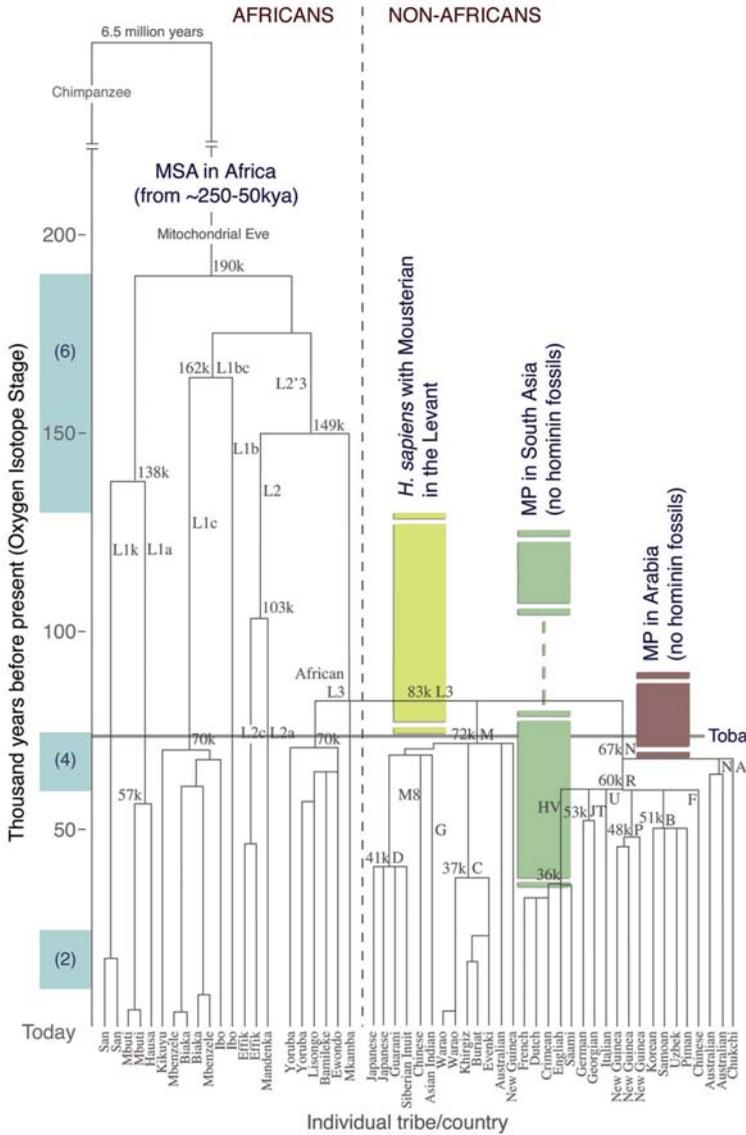
Figure 4. Key ages for Middle Stone Age (MSA)/Mousterian/Middle Palaeolithic (MP) industries and species superimposed on Oppenheimer's (2009: Figure 2) gene-tree, based on first mtDNA complete sequence data.

Once *H. sapiens* colonized India, it is remains unclear if archaic populations (i.e. descendants and contemporaries of the Narmada hominin) were still present in the subcontinent. If this is the case, we surmise that the spread of *H. sapiens* and the indigenous presence of archaic hominins may be marked by Middle Palaeolithic and Late Acheulean industries, respectively. Of course, there is also the possibility that both archaic hominins and *H. sapiens* used Middle Palaeolithic technologies (similar to the evidence that Neandertals and *H. sapiens* in the Levant used Mousterian toolkits). It is unclear if the demise of Neandertals and archaic populations in these regions was the product of reproductive failure or the result of direct competition with *H. sapiens*, though future field work and discoveries will undoubtedly help to resolve this question.

Route of dispersal

The route of Middle Palaeolithic dispersals from the west is likely to have been a complex process. We surmise that the movement of *H. sapiens* out of Africa was probably not as straightforward as implied by the single rapid coastal model. With respect to routes of expansion, Middle Palaeolithic site distributions in Arabia suggest that *H. sapiens* used the Sinai route expanding along the Red Sea to Yemen, or they may also have crossed the Bab al-Mandab from the Horn of Africa, given the presence of sites in southwestern Yemen and along the Arabian Sea coast (Petraglia and Alsharekh 2003). The presence of Levantine-like assemblages at 80–70 ka in Yemen and the presence of MSA-like Sangoan assemblages at >85 ka from UAE indicates that different routes into Arabia may have been used at different times. Certainly, once in Arabia during OIS 5, populations would have spread into the interior using corridors established by the presence of rivers and lakes.

As *H. sapiens* spread eastwards from their base in Arabia, they may have travelled into the interior of the Iranian plateau, or they may have avoided the mountainous areas, skirting along the littoral flanks of the Arabian Sea (Field and Lahr 2005; Field et al. 2007). Mapping the potential corridors in the mountainous and littoral zones of Iran and Pakistan would be of great value for future assessment of dispersal routes, as it is possible that populations reached the subcontinent through different routes. Once present in the sub-Himalayan zone and Indo-Gangetic belt of northern India, it is likely that populations expanded into the interior relatively quickly, using the main river valleys and basins as corridors for movement (Korisettar 2007).

Environmental variation along the Indian Ocean rim

The fluctuation of environments in the Late Pleistocene, which resulted in lake development during humid phases and the expansion of desert landscapes during arid periods, is thought to have played a major role in the expansion, contraction and extinction of human populations (Lahr and Foley 1994). While Middle Palaeolithic hominins appear to have successfully spread across landscapes in the Arabia peninsula, occupations were probably not established over the very long-term on account of expanding desertification. During OIS 4, large expanses of Arabia were not conducive to permanent occupation, as indicated by the development of sand seas and the disappearance of fresh water sources such as lakes. During arid phases, populations foraging along the interior lakes probably either went extinct or moved into refugia in mountainous zones or along the Red Sea, the Arabian Sea and the Gulf. While *H. sapiens* may have been able to adapt to less hostile fluctuations in their environments, during the most arid phases their survival would have been tenuous, perhaps leading to some budding off of populations to other regions. In this scenario, we would expect that Middle Palaeolithic sites and landscapes will not be as dense in Arabia as those in other regions where ecological contexts and natural resources may have been more dependable over the long term, such as in peninsular India.

The environmental and topographic situation in the Indian subcontinent is strikingly different from that in Arabia, primarily on account of the presence of a diversity of flora and fauna and heterogeneous landforms, including geological basins. Though populations in the subcontinent would have had to adjust to climatic and environmental fluctuations, particularly during OIS 4, *H. sapiens* would have been able to survive in a variety of ecological settings, including in large basin settings where freshwater resources and biomass were concentrated. The abundance of Middle Palaeolithic archaeological sites in a number of these basins suggests that populations survived over long intervals and through climatic deteriorations.

Technology and modern human behaviour

The presence of Middle Palaeolithic archaeological sites in Arabia and South Asia is beyond doubt, and we have hypothesized that *H. sapiens* expanded around the geographic regions of the Indian Ocean rim with such prepared core technologies. However, it is impossible to relate Arabian and Indian assemblages to their original geographic source in the absence of systematic, inter-regional lithic comparisons. Our own quantified study of Middle Palaeolithic core technology indicated parallels between peninsular Indian assemblages and those made by *H. sapiens* in the MSA of Africa (Petraglia et al. 2007). One other systematic study, using the chaîne opératoire approach, suggested an affinity between Yemeni and Levantine industries (Crassard 2009). Otherwise, all other assemblage-based inter-regional comparisons remain observational and impressionistic, though this does not invalidate their inferences. Indeed, the argument that some Arabian assemblages resemble Levantine or African MSA industries is significant, suggesting that the dispersal situation is more complicated than currently realized. On the other hand, the view that some Arabian and Indian Middle Palaeolithic assemblages are unique, and may share little technological or stylistic equivalents with their surrounding regions, is interesting from a behavioural perspective, but perhaps frustrating to those who wish to map the source of population movements.

The archaeological record of Arabia and the Indian subcontinent show no rapid or sudden appearance of a modern behavioural package that can be considered to signal a 'human revolution' similar to the Aurignacian in Europe. The record also does not indicate the spread of an Upper Palaeolithic package in the neighbourhood of 60 or 50 ka, when the dispersal of *H. sapiens* is now widely presumed to have taken place. The Arabian Palaeolithic lacks any material signs of symbolic behaviours, though caution is obviously warranted given that the majority of sites in Arabia are known from surface contexts. In a re-evaluation of Arabian sites that have been labelled 'Upper Palaeolithic', Maher (2009) found that these assemblages lack the range of classic types, such as points, carinated pieces, and various blade tools. The recovery of laminar industries in both Middle Palaeolithic and later terminal Pleistocene/Early Holocene assemblages of Arabia should not necessarily be considered the equivalent of Levantine or Western European industries (Marks 2009).

The so-called Upper Palaeolithic industries of South Asia are generally poorly known and some of these assemblages may be very young. The presence of sites with laminar assemblages in South Asia are part of a diverse set of Late Palaeolithic sites (James and Petraglia 2005). We do not, however, consider these laminar technologies to be a sign of an invasive population spread into the subcontinent, but instead these technological innovations appear to be part of an indigenous package that evolves regionally as a consequence of new adaptations. On this score, we have documented that Middle Palaeolithic industries can be found to at least 38 ka, with a major technological transition to blade and microblade industries occurring at about 35–30 ka (Petraglia et al. 2009a). We have argued that the trajectory of 'modern human behaviours' in South Asia is a distinct phenomenon in comparison to other regions. Though gradual and rare, some hallmarks of the modern human behavioural package make their appearance after 45 ka, and increase substantially from 35 ka upwards. The temporally gradual and spatially patchy assembly of modern traits in South Asia is similar to that found in the Australian record, which has been characterized as slow and sporadic in its symbolic construction (Brumm and Moore 2005). The gradual and mosaic-like pattern of change in cultural traits in time and space indicates that material culture developed in fundamentally different ways as *H. sapiens* spread across the southern dispersal zone.

Final conclusion

This review indicates that there is likely still much to learn about the dispersal of *H. sapiens* out of Africa. Though much evidence bearing on dispersal processes has been retrieved in recent years, it is clear that there are major gaps in our current understanding of when, how and why these expansions occurred. This situation calls for the recovery of much on-the-ground evidence to examine the dispersal and evolution of human populations in the Late Pleistocene. It also calls for new genetic sequencing studies that may be useful for better characterizing past population structure. Though we recognize that much research remains to be conducted, we have nevertheless attempted to synthesize current information about the movement of *H. sapiens* along the Indian Ocean rim, providing some alternative interpretations based on new evidence from Arabia and South Asia. Based on our review of the fossil, genetic, and archaeological evidence, we argue that the expansion of *H. sapiens* out of Africa was a complex process, and not simply the consequence of a single, rapid coastal expansion at 60 ka ago. We argue that that modern human expansion into Arabia is probably coincident with the ages of 130–70 ka for *H. sapiens* in the Levant, with populations reaching South Asia by 78 ka, and perhaps earlier. Relatively young mtDNA and Y chromosome coalescence ages are a reflection of re-colonization events in certain areas (e.g. deserts) and major demographic increases in the Late Pleistocene in particular regions (e.g. South Asia), which have had the effect of swamping the gene pools of older and smaller foraging groups. To better understand Pleistocene expansions of human populations along the Indian Ocean rim, we can only hope that much more archaeological research and dating will be conducted in poorly known areas, and that fossils and ancient DNA will be recovered from the many ideal, but presently unexcavated contexts in Arabia and South Asia.

Acknowledgements

Note

1. OIS 5a represents a peak in July insolation at 20N, with CH4 and O18 isotope levels showing a peak towards warmer conditions, although only about half as high as Early Holocene levels, but the most recent high peak in methane prior to the Holocene (Ruddiman 2008: Figures 10-16, 14-8). This implies stronger monsoons than in subsequent OIS 4 (Gasse 2000; Ruddiman 2008). Actual pollen data are limited, but Arabian evidence from ocean core (MD76135) and South Indian evidence from sea cores off the Kerala coast

provide some indication (Van Campo et al. 1982; Prabhu et al. 2004). A partial baseline is taken from mid-Holocene reconstruction of Adams and Faure (1997), but this has been substantially edited by comparing their modern conditions maps with more detailed vegetation maps and taking into account the role of topographic features. For South Asia we used the vegetation data discussed in Puri et al. (1983), Asouti and Fuller (2008), while for the Middle East and Arabia we used Zohary (1973) and Van Zeist and Bottema (1991) and the discussions in Moore et al. (2000). For eastern Africa we considered vegetation zones of Rattray (1960) and the charcoal and pollen-based Holocene reconstructions of Neumann (1991).

MD76135 shows a peak in summed humid tropical indicators at 90 ka, surpassed only by Early Holocene Maximum. Levels show a slight decline towards 80 ka but remain substantial, comparable to the Mid-Holocene. We take this to indicate healthy sub-tropical Abyssinian woodlands in the hills forests of Yemen, Dhofar and Central Oman. Tropical dry elements show an expansion from 90 to 80 ka which is taken to represent expanding dry savanna grassland or Sahelian-like sub-desert on the Arabian peninsula. Rhizophoraceae pollen in core SK128A-30 off the South Indian coast shows a small but consistent presence of Mangrove pollen greater than recent times and comparable to mid-Holocene levels. This indicates generally favourable conditions along coasts throughout this region, which means that Omani coasts are likely to have had more substantial and diverse mangroves than the present day. This could have offered corridors of rich coastal resources.

References

Abu-Amero KK, Gonzalez AM, Larruga, JM, Bosley, TM, Cabrera, VM. 2007. Eurasian and African mitochondrial DNA influences in the Saudi Arabian population. BMC Evol Biol 7:32.

Abu-Amero KK, Larruga JM, Cabrera VM, Gonzalez AM. 2008. Mitochondrial DNA structure in the Arabian peninsula. BMC Evol Biol 8:45.

Achyuthan H, Quade, J, Roe L, Placzek, C. 2007. Stable isotopic composition of pedogenic carbonates from the eastern margin of the Thar Desert, Rajasthan, India. Quatern Int 162-3:50–60.

Adams JH, Faure, H. 1997. Preliminary vegetation maps of the world since the Last Glacial Maximum: An aid to archaeological understanding. J Archaeol Sci 24:623–647.

Allchin BA, Goudie, A, Hegde, K. 1978. The prehistory and palaeogeography of the Great Indian Desert. London: Academic Press.

Alshamali F, Pereira L, Budowle B, Poloni, ES, Currant M. 2009. Local population structure in Arabian peninsula revealed by Y-STR diversity. Hum Hered 68:45–54.

Ambrose SH. 1998. Late Pleistocene human population bottlenecks, volcanic winter and differentiation in modern humans. J Hum Evol 34:623–651.

Amirkhanov H. 1994. Research on the Palaeolithic and Neolithic of Hadhramaut and Mahra. Arab Archaeol Epigraphy 5:217–228.

Asouti E, Fuller DQ. 2008. Trees and woodlands of South India: Archaeological perspectives. Walnut Creek, CA: Left Coast Press.

Athreya S. 2007. Was Homo heidelbergensis in South Asia? A test using the Narmada fossil from central India. In: Petraglia, MD, Allchin B, editors. The evolution and history of human populations in South Asia. Netherlands: Springer, pp. 137–170.

Atkinson QD, Gray RD, Drummond AJ. 2008. mtDNA variation predicts population size in humans and reveals a major Southern Asian chapter in human prehistory. Mol Biol Evol 25:468–474.

Bailey GN. 2009. The Red Sea, coastal landscapes and hominin dispersals. In: Petraglia MD, Rose JI, editors. The evolution of human populations in Arabia. Netherlands: Springer, pp. 15–37.

Barik SS, Sahani R, Prasad BVR, Endicott P, Metspalu M, Sarkar BN, Bhattacharya S, Annapoorna PCH, Sreenath J, Sun D, Sanchez JJ, Ho SYW, Chandrasekar A, Rao VR. 2008. Detailed mtDNA genotypes permit a reassessment of the settlement and population structure of the Andaman Islands. Am J Phys Anthropol 136:19–27.

Barker G, Barton H, Bird M, Daly P, Datan I, Dykes A, Farr L, Gilbertson D, Harrisson B, Hunt C, Higham T, Kealhofer L, Krigbaum J, Lewis H, McLaren S, Paz V, Pike A, Piper P, Pyatt B, Rabett R, Reynolds T, Rose J, Rushworth G, Stephens M, Stringer C, Thompson J, Turney C. 2007. The 'human revolution' in lowland

tropical Southeast Asia: The antiquity and behavior of anatomically modern humans at Niah Cave (Sarawak, Borneo). J Hum Evol 52:243–261.

Bar-Yosef O. 2007. The archaeological framework of the Upper Paleolithic revolution. Diogenes 54:3–18.

Bellwood P. 2005. First farmers: The origins of agricultural societies. Oxford: Blackwell.

Beyin A. 2006. The Bab al Mandb vs the Nile-Levant: An appraisal of the two dispersal routes for early modern humans out of Africa. Afr Archaeol Rev 23:5–30.

Boivin N, Blench R, Fuller DQ. 2009. Archaeological, linguistic and historical sources on ancient seafaring: A multidisciplinary approach to the study of early maritime contact and exchange in the Arabian peninsula. In: Petraglia MD, Rose JI, editors. The evolution of human populations in Arabia. Netherlands: Springer, pp. 251–278.

Brumm A, Moore M. 2005. Symbolic revolutions and the Australian archaeological record. Cambridge Archaeol J 15:157–175.

Bulbeck D. 2007. Where river meets sea: A parsimonious model for Homo sapiens colonization of the Indian Ocean rim and Sahul. Curr Anthropol: 315–321.

Cabrera VM, Abu-Amero KK, Larruga JM, González AM. 2009. The Arabian peninsula: Gate for human migrations out of Africa or cul-de-sac? A mitochondrial DNA phylogeographic perspective. In: Petraglia MD, Rose JI, editors. The evolution of human populations in Arabia. Netherlands: Springer, pp. 79–87.

Cameron D, Patnaik R, Sahni A. 2004. The phylogenetic significance of the Middle Pleistocene Narmada hominin cranium from central India. Int J Osteoarchaeol 14:419–447.

Cerny V, Mulligan CJ, Rídl J, Žaloudková M, Edens C, Hájek M, Pereira L. 2008. Regional differences in the distribution of the Sub-Saharan, West Eurasian and South Asian mtDNA lineages in Yemen. Am J Phys Anthropol 136:128–137.

Churchill SE. 1998. Cold adaptation, heterochrony, and Neandertals. Evolutionary Anthropol 7:46–61.

Clarkson C, Petraglia M, Korisettar R, Haslam M, Boivin N, Crowther A, Ditchfield P, Fuller D, Miracle P, Harris C, Connell K, James H, Koshy J. 2009. The oldest and longest enduring microlithic sequence in India: 35 000 years of modern human occupation and change at the Jwalapuram Locality 9 rockshelter. Antiquity 83:326–348.

Cleuziou S, Inizan M-L, Marcolongo B. 1992. Le peuplement pré- et protohistorique du système fluviatile fossile du Jawf-Hadramawt au Yémen (d'après l'interprétation d'images satellite, de photographies aériennes et de prospections). Paléorient 18:5–29.

Crassard R. 2009. The Middle Paleolithic of Arabia: The view from the Hadramawt region, Yemen. In: Petraglia MD, Rose JI, editors. The evolution of human populations in Arabia. Netherlands: Springer, pp. 151–168.

Delagnes A, Macchiarelli R, Jaubert J. 2008. Middle Paleolithic settlement in Arabia: First evidence from a complex of stratified archaeological sites in western Yemen. Paper presented at Palaeoanthropology Meetings, Vancouver.

Deraniyagala SU. 1992. The prehistory of Sri Lanka: An ecological perspective. Colombo: Department of the Archaeological Survey, Government of Sri Lanka.

Edgell HS, 2006. Arabian deserts: Nature, origin and evolution. Amsterdam: Springer.

Endicott P, Gilbert M, Stringer C, Lalueza-Fox C, Willerslev E, Hansen A, Cooper A. 2003. The genetic origins of the Andaman Islanders. Am J Hum Genet 72:178–184.

Endicott P, Metspalu M, Kivisild T. 2007. Genetic evidence on modern human dispersals in South Asia: Y chromosome and mitochondrial DNA perspectives: The world through the eyes of two haploid genomes. In: Petraglia MD, Allchin B, editors. The evolution and history of human populations in South Asia. Amsterdam: Springer, pp. 229–244.

Endicott P, Ho SYW, Metspalu M, Stringer C. 2009. Evaluating the mitochondrial timescale of human evolution. Trends Ecol Evol 24:515–521.

Fernandes C. 2009. Bayesian coalescent inference from mitochondrial DNA variation of the colonization time of Arabia by the hamadryas baboon (*Papio hamadryas hamadryas*). In: Petraglia MD, Rose JI, editors. The evolution of human populations in Arabia. Amsterdam: Springer, pp. 89–100.

Field JS, Lahr MM. 2005. Assessment of the southern dispersal: GIS-based analyses of potential routes at Oxygen Isotopic Stage 4. J World Prehistory 19:1–45.

Field J, Petraglia MD, Lahr MM. 2007. The southern dispersal hypothesis and the South Asian archaeological record: Examination of dispersal routes through GIS analysis. J Anthropol Archaeol 26:88–108.

Finlayson C, Carrión JS. 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. Trends Ecol Evol 22:213–222.

Fleitmann D, Matter A. 2009. The speoleothem record of climate variability in southern Arabia. CR Geoscience, in press.

Foley RA, Lahr MM. 1997. Mode 3 technologies and the evolution of modern humans. Cambridge Archaeol J 7:3–36.

Forster P, Torroni A, Renfrew C, Röhl A. 2001. Phylogenetic star contraction applied to Asian and Papuan mtDNA evolution. Mol Biol Evol 18:1864–1881.

Forster P, Matsumura S. 2005. Did early humans go north or south? Science 308:965–966.

Garrard AN, Harvey CPD, Switsur VR. 1981. Environment and settlement during the Upper Pleistocene and Holocene at Jubba in the Great Nefud, Northern Arabia. Atlal 5:137–148.

Garrigan D, Hammer MF. 2006. Reconstructing human origins in the genomic era. Nat Rev Genet 7:669–680.

Gasse F. 2000. Hydrological changes in the African tropics since the last glacial maximum. Quatern Sci Rev 19:189–211.

Gilmore M, Al-Ibrahim M, Murad AS. 1982. 1 – preliminary report on the northwestern and northern region survey 1981 (1401). Atlal 6:9–23.

Glennie KW, Singhvi AK. 2002. Event stratigraphy, paleoenvironment and chronology of SE Arabian deserts. Quatern Sci Rev 21:853–869.

González AM, Larruga JM, Abu-Amero KK, Shi Y, Pestano J, Cabrera VM. 2007. Mitochondrial lineage M1 traces an early human backflow to Africa. BMC Genomics 8:223.

Gunz P, Bookstein FL, Mitteroecker P, Stadlmayr A, Seidler H, Weber GW. 2009. Early modern human diversity suggests subdivided population structure and a complex out-of-Africa scenario. Proc Natl Acad Sci 106:6094–6098.

Ingman M, Kaessmann H, Paabo S, Gyllensten D. 2000. Mitochondrial genome variation and the origin of modern humans. Nature 408:708–713.

Inizan M-L, Ortlieb L. 1987. Préhistoire dans la région de Shabwa au Yemen du sud (R.D.P. Yemen). Paléorient 13:5–22.

Inizan M-L, Lezine A-M, Marcolongo B, Saliege J-F, Robert C, Werth F. 1998. Paléolacs et peuplements Holocènes du Yémen: le Ramlat As-Sabat'Ayn. Paléorient 23:137–149.

James HVA. 2007. The emergence of modern human behavior in South Asia. In: Petraglia MD, Allchin B, editors. The evolution and history of human populations in South Asia. Amsterdam: Springer, pp. 201–227.

James HVA. 2009. Becoming human: The emergence of modern human behaviour in South Asia. PhD dissertation, University of Cambridge, Cambridge.

James HVA, Petraglia MD. 2005. Modern human origins and the evolution of behavior in the later Pleistocene record of South Asia. Curr Anthropol 46:S3–27.

James H, Petraglia MD. 2009. The Lower to Middle Paleolithic transition in South Asia and its implications for hominin cognition and dispersals. In: Camps M, Chauhan P, editors. Sourcebook of Paleolithic transitions. New York: Springer, pp. 255–264.

Jayaswal, V. 1978. Palaeohistory of India: A study of the prepared core technique. Delhi: Agam Kala Prakashan.

Jones S. 2007. The Toba supervolcanic eruption: Tephra fall deposits in India and paleoanthropological implications. In: Petraglia MD, Allchin B, editors. The evolution and history of human populations in South Asia. Amsterdam: Springer, pp. 173–200.

Kennedy, KAR. 2000. God apes and fossil men: Paleoanthropology in South Asia. Ann Arbor: University of Michigan Press.

Kivisild T, Kaldma K, Metspalu M, Parik J, Papiha SS, Villems RR. 1999. The place of the Indian mitochondrial DNA variants in the global network of maternal lineages and the peopling of the Old World. In: Papiha SS, Deka R, Chakraborty R, editors. Genomic diversity. New York: Kluwer Academic/Plenum, pp. 135–152.

Kivisild T, Papiha SS, Rootsi S, Parik J, Kaldma K, Reidla M, Laos S, Metspalu M, Pielberg G, Adojaan M, Metspalu E, Mastana SS, Wang Y, Gölge M, Demirtas H, Schnakenberg E, Franco de Stefano G, Geberhiwot T, Claustres M, Villems R. 2000. An Indian ancestry: A key for understanding human diversity in Europe and beyond. In: Renfrew C, Boyle K, editors. Archaeogenetics: DNA and the population history of Europe. Cambridge: McDonald Institute for Archaeological Research, pp. 267–275.

Kivisild T, Rootsi S, Metspalu M, Mastana S, Kaldma K, Parik J, Metspalu E, Adojaan M, Tolk H-V, Stepanov V, Gölge M, Usanga E, Papiha SS, Cinnioğlu C, King R, Cavalli-Sforza L, Underhill PA, Villems R. 2003. The genetic heritage of the earliest settlers persists both in Indian tribal and caste populations. Am J Hum Genet 72:313–332.

Kivisild T, Reidla M, Metspalu E, Rosa A, Brehm A, Pennarum E, Parik J, Geberhiwot T, Usanga E, Villems R. 2004. Ethiopian mitochondrial heritage: Tracking gene flow across and around the Gate of Tears. Am J Hum Genet 75:752–770.

Klein R. 2000. Archeology and the evolution of human behavior. Evol Anthropol 9:17–36.

Korisettar R. 2007. Towards developing a basin model for the Paleolithic settlement of the Indian subcontinent: Geodynamics, monsoon dynamics and dispersal routes. In: Petraglia MD, Allchin B, editors. The evolution and history of human populations in South Asia. Amsterdam: Springer, pp. 69–96.

Kumar S, Ravuri RR, Koneru P, Urade BP, Sarkar BN, Chandrasekar A, Rao VR. 2009. Reconstructing Indian–Australian phylogenetic link. BMC Evol Biol 9:173.

Lahr MM, Foley RA. 1994. Multiple dispersals and modern human origins. Evol Anthropol 3:48–60.

Lahr MM, Foley RA. 1998. Towards a theory of modern human origins: Geography, demography, and diversity in recent human evolution. Yearbook Phys Anthropol 41:137–176.

Luis J, Rowold D, Regueiro M, Caeiro B, Cinnioğlu C, Roseman C, Underhill P, Cavalli-Sforza L, Herrera R. 2004. The Levant versus the Horn of Africa: Evidence for bidirectional corridors of human migrations. Am J Hum Genet 74:532–544.

Macaulay V, Hill C, Achilli A, Rengo C, Clarke D, Meehan W, Blackburn J, Semino O, Scozzari R, Cruciani F, Taha A, Shaari NK, Raja JM, Ismail P, Zainuddin X, Goodwin W, Bulbeck D, Bandelt HJ, Oppenheimer S, Torroni A, Richards M. 2005. Single, rapid coastal settlement of Asia revealed by analysis of complete mitochondrial genomes. Science 308:1034–1036.

Maca-Meyer N, González AM, Larruga JM, Flores C, Cabrera VM. 2001. Major genomic mitochondrial lineages delineate early human expansions. BMC Genet 2:13.

Macchiarelli R. 2008. From Africa to Asia through Arabia: Models, predictions, and witnesses of first phases of human settlement. Paper presented at the Conference on the First Great Migrations of Peoples, UNESCO, Paris.

Maher L. 2009. The Late Pleistocene of Arabia in relation to the Levant. In: Petraglia MD, Rose JI, editors. The Evolution of Human Populations in Arabia. Netherlands: Springer, pp. 187–202.

Majumder PP. 2001. Ethnic populations of India as seen from an evolutionary perspective. J Biosci 26:533–545.

Marathe, AR. 1981. Geoarchaeology of the Hiran Valley, Saurashtra, India. Poona: Deccan College Postgraduate and Research Institute.

Marks A. 2009. The Paleolithic of Arabia in an inter-regional context. In: Petraglia MD, Rose JI, editors. The Evolution of Human Populations in Arabia. Amsterdam: Springer, pp. 295–308.

McClure H. 1976. Radiocarbon chronology of late Quaternary lakes in the Arabian desert. Nature 263:755–756.

McClure H. 1978. Al-Rub' al-Khali. In: Al-Sayari SS, Zötl JG, editors. Quaternary Period in Saudi Arabia. New York: Springer, pp. 252–263.

McClure H. 1994. A new Arabian stone tool assemblage and notes on the Aterian industry of North Africa. Arabian Archaeol Epigraphy 5:1–16.

McDougall I, Brown F, Fleagle J. 2005. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. Nature 433:733–736.

Mellars P. 2006a. Going East: New genetic and archaeological perspectives on the modern human colonization of Eurasia. Science 313:796–800.

Mellars P. 2006b. Why did modern humans populations disperse from Africa ca. 60,000 year ago? A new model. Proc Natl Acad Sci 103/25:9381–9386.

Metspalu M, Kivisild T, Metspalu E, Parik J, Hudjashov G, Kaldma K, Serk P, Karmin M, Behar DM, Gilbert MTP, Endicott P, Mastana S, Papiha SS, Skorecki K, Torroni A, Villems R. 2004. Most of the extant mtDNA boundaries in South and Southwest Asia were likely shaped during the initial settlement of Eurasia by anatomically modern humans. BMC Genet 5:26.

Misra VN. 1967. Pre-and Proto-history of the Berach Basin south Rajasthan. Poona: University of Poona.

Misra VN. 1968. Middle Stone Age in Rajasthan. In: Bordes F, de Sonneville Bordes D, editors. La Préhistoire, Problèmes et Tendancies. Paris: Centre National de la Recherché Scientifique, pp. 295–305.

Misra VN. 1985. The Acheulean succession at Bhimbetka, central India. In: Misra VN, Bellwood P, editors. Recent advances in Indo-Pacific prehistory. New Delhi: Oxford IBH, pp. 35–47.

Misra VN. 1989. Stone Age India: An ecological perspective. Man Environ XIV:17–64.

Misra VN. 1995a. Geoarchaeology of the Thar Desert, North West India. In: Wadia S, Korisettar R, Kale VS, editors. Quaternary environments and geoarchaeology of India. Bangalore: Geological Society of India, pp. 210–230.

Misra VN. 1995b. The evolution of environment and culture in the Rajasthan desert during the Late Quaternary. In: Johnson E, editor. Ancient peoples and landscapes. Lubbock, TX: Texas Tech University Press, pp. 77–103.

Misra VN. 2001. Prehistoric human colonization of India. J Biosci 26:491–531.

Moore A, Hillman G, Legge A. 2000. Village on the Euphrates: From foraging to farming at Abu Hureyra. New York: Oxford University Press.

Murty MLK. 1979. Recent research on the Upper Palaeolithic phase in India. J Field Archaeol 6:301–320.

Neumann K. 1991. In search of the green Sahara: Palynology and botanical macro-remains. Palaeoecol Africa 22:203–212.

O'Connell JF, Allen J, 2004. Dating the colonization of Sahul (Pleistocene Australia–New Guinea): A review of recent research. J Archaeol Sci 31:835–853.

Olivieri A, Achilli A, Pala M, Battaglia V, Fornarino S, Al-Zahery N, Scozzari R, Cruciani F, Behar DM, Dugoujon J-M, Coudray C, Santachiara-Benerecetti AS, Semino O, Bandelt H-J, Torroni A. 2006. The mtDNA legacy of the Levantine Early Upper Palaeolithic in Africa. Science 314:1767–1770.

Oppenheimer, S. 2003. Out of Eden: The peopling of the world. London: Constable.

Oppenheimer S. 2009. The great arc of dispersal of modern humans: Africa to Australia. Quatern Int 202:2–13.

Paddayya K. 1984. India. In: Bar-Yosef O, editor. Neue Forschungen Zur-Altsteinzeit. Munich: Verley C H Beck, pp. 345–403.

Pappu, RS, Deo SG. 1994. Man–land relationships during Palaeolithic times in the Kaladgi Basin, Karnataka. Pune: Deccan College.

Parker A, Rose J. 2008. Climate change and human origins in southern Arabia. Proc Semin Arabian Stud 38:25–42.

Parr PJ, Zarins J, Ibrahim M, Waechter J, Garrard A, Clarke C, Bidmead M, al-Badr H. 1978. Preliminary report on the second phase of the northern province survey 1397/1977. Atlal 2:29–50.

Patnaik R, Chauhan PR, Rao MR, Blackwell BAB, Skinner AR, Sahni A, Chauhan MS, Khan HS. 2009. New geochronological, paleoclimatological, and archaeological data from the Narmada Valley hominin locality, central India. J Hum Evol 56:114–133.

Petraglia MD. 2007. Mind the gap: Factoring the Arabian peninsula and the Indian subcontinent into Out of Africa models. In: Mellars P, Boyle K, Bar-Yosef O, Stringer C, editors. Rethinking the human revolution. Cambridge: McDonald Institute Monographs, pp. 383–394.

Petraglia M, Korisettar R, Boivin N, Clarkson C, Ditchfield P, Jones S, Koshy J, Lahr MM, Oppenheimer C, Pyle D, Roberts R, J-L Schwenninger, Arnold L, White K. 2007. Middle Palaeolithic assemblages from the Indian subcontinent before and after the Toba super-eruption. Science 317:114–116.

Petraglia, MD, Allchin B (Eds). 2007. The evolution and history of human populations in South Asia. Amsterdam: Springer.

Petraglia MD, Alsharekh A. 2003. The Middle Palaeolithic of Arabia: Implications for modern human origins, behaviour and dispersals. Antiquity 77:671–684.

Petraglia, MD, Rose J (Eds). 2009. The evolution of human populations in Arabia. Amsterdam: Springer.

Petraglia MD, Schuldenrein J, Korisettar R. 2003. Landscapes, activity, and the Acheulean to Middle Paleolithic transition in the Kaladgi Basin, India. Eurasian Prehist 1:3–24.

Petraglia M, Clarkson C, Boivin N, Haslam M, Korisettar R, Chaubey G, Ditchfield P, Fuller D, James H, Jones S, Kivisild T, Koshy J, Lahr MM, Metspalu M, Roberts R, Arnold L. 2009a. Population increase and environmental deterioration correspond with microlithic innovations in South Asia ca. 35,000 years ago. Proc Natl Acad Sci 106:12261–12266.

Petraglia M, Korisettar R, Kasturi Bai M, Boivin N, B J, Clarkson C, Cunningham K, Ditchfield P, Fuller D, Hampson J, Haslam M, Jones S, Koshy J, Miracle P, Oppenheimer C, Roberts R, White K. 2009b. Human occupation, adaptation and behavioral change in the Pleistocene and Holocene of South India: Recent investigations in the Kurnool District, Andhra Pradesh. Eurasian Prehist 6:119–166.

Prabhu C, Shankar R, Anupama A, Taieb M, Bonnefille RR, Vidal L, Prasad S. 2004. A 200-ka pollen and oxygen isotopic record from two sediment cores from the eastern Arabian Sea. Palaeogeograph Palaeoclimatol Palaeoecol 214:309–321.

Preusser F. 2009. Chronology of the impact of Quaternary climate change on continental environments in the Arabian peninsula. CR Geosci, in press.

Puri G, Gupta R., Meher-Homji V. 1983. Forest ecology, 2nd ed., volume I: Phytogeography and forest conservation. Delhi: Oxford and IBH.

Quintana-Murci L, Semino O, Bandelt HJ, Passarino G, McElreavey K, Santachiara-Benerecetti S. 1999. Genetic evidence for an early exit of *Homo sapiens sapiens* from Africa through eastern Africa. Nat Genet 23:437–441.

Rath A, Reddy, KT, Vijaya Prakash PV. 1997. Middle Palaeolithic assemblage from Ramayogi Agraharam in the red sediments in the Visakhapatnam Coast. Man Environ XXII:31–38.

Rattray J. 1960. The grass cover of Africa. Rome: FAO.

Richards M, Rengo C, Cruciani F, Gratrix F, Wilson JF, Scozzari R, Macaulay V, Torroni A. 2003. Extensive female-mediated gene flow from sub-Saharan Africa into near eastern Arab populations. Am J Hum Genet 72:1058–1064.

Rídl J, Edens CM, Cerny V. 2009. Mitochondrial DNA structure of Yemeni population: Regional differences and the implications for different migratory contributions. In: Petraglia MD, Rose JI, editors. The evolution of human populations in Arabia. Amsterdam: Springer, pp. 69–78.

Rohling EJ, Fenton M, Jorissen FJ, Bertrand P, Ganssen G, Caulet JP. 1998. Magnitudes of sea-level lowstands of the past 500,000 years. Nature 394:162–165.

Rose JI. 2004a. The question of Upper Pleistocene connections between East Africa and South Arabia. Curr Anthropol 45:551–556.

Rose JI. 2004b. New evidence for the expansion of an Upper Pleistocene population out of East Africa, from the site of Station One, Northern Sudan. Cambridge Archaeol J 14:205–216.

Rose JI, Petraglia MD. 2009. Tracking the origin and evolution of human populations in Arabia. In: Petraglia MD, Rose JI, editors. The evolution of human populations in Arabia. Amsterdam: Springer, pp. 1–12.

Rose JI, Usik VI. 2009. The 'Upper Paleolithic' of South Arabia. In: Petraglia MD, Rose JI, editors. The evolution of human populations in Arabia. Amsterdam: Springer, pp. 169–186.

Rowland DJ, Luis JR, Terreros MC, Herrera RJ. 2007. Mitochondrial DNA geneflow indicates preferred usage of the Levant corridor over the Horn of Africa passageway. J Hum Genet 52:436–447.

Roychoudhury S, Roy S, Dey B, Chakraborty M, Roy M, Roy B, Ramesh A, Prabhakaran N, Rani MVU, Vishwanathan HM, Mitra M, Sil SK, Majumder PP. 2000. Fundamental genomic unity of ethnic India is revealed by analysis of mitochondrial DNA. Curr Sci 79:1182–1192.

Roychoudhury S, Roy S, Basu A, Banerjee R, Vishwanathan H, Rani MVU, Sil SK, Mitra M, Majumder PP. 2001. Genomic structures and population histories of linguistically distinct tribal groups of India. Hum Genet 109:339–350.

Ruddiman W. 2008. Earth's climate: Past and future, 2nd ed. New York: Freeman.

Sharma GR, Clark, JD. 1983. Palaeoenvironments and prehistory in the Middle Son Valley. Allahabad: Abinash Prakashan.

Shea JJ. 2001. The Middle Paleolithic: Early modern humans and Neandertals in the Levant. Near Eastern Archaeol 64(1–2):38–64.

Shea JJ. 2008. Transitions or turnovers? Climatically-forced extinctions of *Homo sapiens* and Neanderthals in the east Mediterranean Levant. Quatern Sci Rev 27:2253–2270.

Soares P, Ermini L, Thomson N, Mormina M, Rito T, Rohl A, Salas A, Oppenheimer S, Macaulay V, Richards MB. 2009. Correcting for purifying selection: An improved human mitochondrial molecular clock. Am J Hum Genet 84:740–749.

Sonakia A. 1985. Skull cap of an early man from the Narmada valley alluvium (Pleistocene) of central India. Am Anthropol 87:612–616.

Sun C, Kong Q-P, Palanichamy MG, Agrawal S, Bandelt H-J, Yao Y-G, Khan F, Zhu C-L, Chaudhuri TK, Zhang Y-P. 2006. The dazzling array of basal branches in the mtDNA macrohaplogroup M from India as inferred from complete genomes. Mol Biol Evol. 23:683–690.

Thangaraj K, Chaubey G, Kivisild T, Reddy AG, Singh VK, Rasalkar AA, Singh, LL. 2005. Reconstructing the origin of Andaman Islanders. Science 308:996.

Torroni A, Achillia A, Macaulay V, Richards M, Bandelt H-K. 2006. Harvesting the fruit of the human mtDNA tree. Trends in Genetics 22:339–345.

Trivedi R, Sahoo S, Singh A, Hima Bindu G, Banerjee J, Tandon M, Gaikwad S, Rajkumar R, Sitalaximi T, Ashma R, Chainy GBN, Kashyap VK. 2008. Genetic imprints of Pleistocene origin of Indian populations: A comprehensive phylogeographic sketch of Indian Y-chromosomes. Int J Hum Genet 8:97–118.

Van Campo E, Duplessy J, Rossignol-Stick M. 1982. Climatic conditions deduces from 150-kyr oxygen isotope-pollen record from the Arabian Sea. Nature 296:56–59.

Van Zeist W, Bottema S. 1991. Late Quaternary vegetation of the Near East. Wiesbaden: Reichart.

Wahida G, Al-Tikriti WY, Beech MJ, Al Meqbali A. 2009. A Middle Paleolithic assemblage from Jebel Barakah, coastal Abu Dhabi Emirate. In: Petraglia MD, Rose JI, editors. The evolution of human populations in Arabia. Amsterdam: Springer, pp. 117–124.

Whalen NM, Pease DW. 1992. Archaeological survey in southwest Yemen, 1990. Paléorient 17/2:129–133.

Whalen N, Killick A, James N, Morsi G, Kamal M. 1981. Saudi Arabian archaeological reconnaissance 1980: b. preliminary report on the western province survey. Atlal 5:43–58.

Whalen NM, Siraj-Ali J, Sindi HO, Pease DW, Badein MA. 1988. A complex of sites in the Jeddah–Wadi Fatimah area. Atlal 11:77–85.

White T, Asfaw B, DeGusta D, Gilbert H, Richards G, Suwa G, Clark Howell F. 2003. Pleistocene Homo sapiens from Middle Awash, Ethiopia. Nature 423:742–747.

Zarins J, Whalen N, Ibrahim M, Jawad Mursi AA, Khan M. 1980. Comprehensive archaeological survey program, preliminary report on the central and southwestern provinces survey: 1979. Atlal 4:9–36.

Zarins J, al-Jawad Murad A, Al-Yish KS. 1981. The comprehensive archaeological survey program. a. The second preliminary report on the Southwestern Province. Atlal 5:9–42.

Zohary M. 1973. Geobotanical foundations of the Middle East. Amsterdam: Swets and Zeitlinger.