



The dispersal of *Homo sapiens* across southern Asia: how early, how often, how complex?

Robin Dennell^{a,*}, Michael D. Petraglia^b

^a Department of Archaeology, University of Sheffield, Sheffield S1 4ET, UK

^b School of Archaeology, University of Oxford, Oxford OX1 3QY, UK

ARTICLE INFO

Article history:

Received 13 March 2012

Accepted 2 May 2012

Available online 12 June 2012

Keywords:

Out of Africa 2

Homo sapiens

Dispersal

Southern Asia

Levant

India

SE Asia

Australia

ABSTRACT

The timing and the paths of colonization of southern Asia by *Homo sapiens* are poorly known, though many population geneticists, paleoanthropologists, and archaeologists have contended that this process began with dispersal from East Africa, and occurred between 60,000 and 40,000 years ago. However, the evidence for this scenario is very weak, particularly the lack of human skeletal evidence between the Levant and Borneo before 40 ka, and other explanations are possible. Here we argue that environmental and archaeological information is increasingly indicating the likelihood that *H. sapiens* exited Africa much earlier than commonly thought, and may have colonized much of southern Asia well before 60,000 years ago. Additionally, we cannot exclude the possibility that several dispersal events occurred, from both North and East Africa, nor the likelihood that early populations of *H. sapiens* in southern Asia interbred with indigenous populations of Neanderthals, Denisovans and *Homo erectus*. The population history of southern Asia during the Upper Pleistocene is likely far more complex than currently envisaged.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Although the expansion of our species from Africa into Europe between 30 and 40 ka has been extensively investigated for over a century, far less is known about its earlier expansion across southern Asia from Arabia to Australia. Over the last few years, a consensus has arisen that this expansion probably occurred between 40 and 60 ka (see e.g. Pettitt, 2005; Klein, 2009). Although opinion is far from unanimous, many palaeoanthropologists would support most components of the following consensus view of how and when this occurred: *Homo sapiens* originated in East Africa by 195–160 ka (White et al., 2003; McDougall et al., 2005), but did not enter Southwest Asia until the Last Interglacial, when it is first evidenced outside Africa by skeletal evidence from the caves of Skhül and Qafzeh in the Levant (McDermott et al., 1993), at ca 100 ka or perhaps as early as 125 ka, at the beginning of the Last Interglacial (Frumkin et al., 2011). It remained there until ca 65 ka when it was replaced by Neanderthals (Shea, 2008), who may have been forced southwards by the increasingly harsh conditions of MIS 4. In this scenario, after being present in the Levant for ca 35–60 ka,

these early populations of *H. sapiens* went extinct, thus leading to the argument that this was a failed dispersal (Shea, 2008; Oppenheimer, 2011) by a group of humans that were not as socially and cognitively advanced as later populations of *H. sapiens* (Mellars, 2006). Following an assumed demographic increase of populations in Africa (Forster, 2004), *H. sapiens* expanded across southern Asia at some point between 40 and 60 ka (Macauley et al., 2005), and those that reached Sundaland – the landmass of modern island Southeast Asia that was linked to the Malaysian peninsula because of lowered sea-levels – eventually crossed the open-sea to enter Australia. Some researchers have suggested that modern humans were the first to exploit systematically coastal resources (notably shell-fish, sea mammals and inshore fish) and were thus able to disperse rapidly along a coastal route (Stringer, 2000; Field and Lahr, 2006), possibly by utilising coastal springs that emerged when sea levels fell (Faure et al., 2002), and thus bypassing indigenous populations that lived further inland. By this means, they were able to reach Australia by ~40 ka (O'Connell and Allen, 2004), or even ~60 ka (Roberts et al., 1994), depending upon which dates are preferred from the Australian mainland.

Although this consensus enjoys widespread support, we suggest that it is best regarded as a series of potentially falsifiable hypotheses, and we should thus be open-minded about alternative perspectives on what is likely to have been a much more complex process of colonisation. Leaving aside for the moment recent

* Corresponding author. Tel.: +44 7799383325.

E-mail addresses: r.dennell@sheffield.ac.uk (R. Dennell), michael.petraglia@rlaha.ox.ac.uk (M.D. Petraglia).

archaeological and skeletal evidence from southern Asia, there are two principal reasons why the current consensus may be overly simplistic. The first stems from its own internal weaknesses as a model, and the second is that the context in which early human dispersals across southern Asia is discussed is changing because of the implications of new fossil and archaeological evidence from Northeast Africa, and the evidence from ancient DNA (aDNA) studies that early *H. sapiens* outside Africa interbred with indigenous populations. To take each in turn:

1.1. Limitations of the current model

The current model for the expansion of *H. sapiens* across southern Asia is based on three lines of evidence: human skeletal material; genetic studies of modern populations; and the timing of arrival of *H. sapiens* in Australia. It has the following internal weaknesses:

1.1.1. The limitations of the human skeletal fossil record

As indicated above, current evidence indicates that *H. sapiens* appeared in east Africa by ca 195–160 ka, whereas the earliest outside Africa are those from Israel at about 100–125 ka ago. At present, there are no hominin fossils 200 ka old from southern Asia, so it is an open question as to when *H. sapiens* first appeared in this region. For Southwest Asia, the specimen from Zuttiyeh Cave, Israel, has been dated by TL to 148 ± 6 ka (Schwarcz et al., 1980), but it may be as old as 300 ka (Bar-Yosef, 1988) and is thus not relevant here; in any case, it is not particularly diagnostic (Sohn and Wolpoff, 1993). The mandible and skeleton from layer C at Tabun cave are usually classified as Neanderthal (Schwartz and Tattersall, 2003: 384; Stefan and Trinkhaus, 1998); this layer has been dated to 165 ± 16 ka by TL on burnt flint (Mercier et al., 2000) and 140 ± 21 ka by ESR (Grün and Stringer, 2000). However, Howell (1996) classified the mandible as *H. sapiens*, and the skeleton was probably an intrusive burial from the overlying layer B (Bar-Yosef and Callander, 1999), dated to 122 ± 16 ka (Grün and Stringer, 2000). There is no fossil evidence of *H. sapiens* (or any other type of hominin) from the Arabian Peninsula prior to the Holocene. All we know at present about southwest Asian hominins between 250 and 125 ka ago is that Neanderthals were present in the northern Levant during part of MIS 6.

In India, the only hominin specimen is that from Hathnora (Narmada Valley), which is best classified as *Homo* sp. indet. (Athreya, 2007) and may be as young as 48 ± 1 ka or as old as 236 ka (Patnaik et al., 2009). In mainland Southeast Asia, the only human skeletal evidence from the late Middle Pleistocene are a few isolated teeth from the Vietnamese caves of Tham Khuyen, Tham Hai, Lang Trang and Hang Hum that are described as hominid (Schwartz et al., 1995), and two teeth of “archaic” *Homo* sp. and an occiput fragment from Ma U’Oi, Vietnam (Demeter et al., 2004, 2005; Bacon et al., 2006), and a similar “archaic” tooth from the cave of Thum Wikan Nakin (Tougaard et al., 1998). In Sundaland (i.e., modern island Southeast Asia), *Homo erectus* was thought to have persisted into the last glaciation on the basis of isotopic dates for the Ngandong (Solo) assemblage of 28–54 ka (Swisher et al., 1996), but a recent study (Indriati et al., 2011) now indicates that the likely age is between 143 and 546 ka. These estimates are consistent with faunal evidence that this hominin assemblage is late Middle Pleistocene in age (Storm, 2001). The earliest unambiguous evidence in Southeast Asia, for *H. sapiens* is the cranium from Niah Cave, Borneo, dated to ca 35–37 ^{14}C ka (40–44 cal ka BP) (Barker et al., 2007). The age of this specimen is comparable to that of the partial skeleton of *H. sapiens* from Tianyudong, North China, and the 32 ka-old *H. sapiens* cranium from Yamashita-cho, Okinawa (Kaifu and Fujita, 2012). Additionally, the 42 ka assemblages from

Timor (O’Connor, 2007), which would most likely have been colonised by using boats or rafts with sails and paddles can also be attributed to *H. sapiens*. Because the earliest evidence from the highlands of New Guinea now extends back to 49 ka (Summerhayes et al., 2010), modern humans must have been on the Sunda Shelf and in mainland Southeast Asia by at least 50 ka. This observation is consistent with the evidence of humans at Tabon Cave, Palawan Island, the southern Philippines. Here, a mandibular fragment has been dated by U-series to $31 + 8/-7$ ka, and a tibia fragment to $47 + 11/-10$ ka (Détroit et al., 2004). Although a maximum age of 58 ka for the tibia might be considered as unacceptable, an age of <50 ka is consistent with the recent evidence from New Guinea.

As with India, the absence of *H. sapiens* from Southeast Asia before 50–60 ka is far from certain, and it is currently an unproven assumption that *H. sapiens* was absent from Southwest, South and mainland Southeast Asia before this time. As noted in relation to the evidence for Out of Africa 1, absence of evidence is not evidence of absence (Dennell and Roebroeks, 2005).

1.1.2. Stone tools are poor indicators of population changes

In the Levant, both Neanderthals and *H. sapiens* used Mousterian stone-tool assemblages, and in East and North Africa, early *H. sapiens* used the same lithic tool-kits as their predecessors. This indicates that stone tools are a poor indicator of the species of the hominin that made them: changes in hominin type did not necessarily result in changes in lithic technology. Conversely, unchanging lithic traditions need not imply that the type of hominin that used them remained the same. As example, in mainland and island Southeast Asia, there is no equivalent of the Upper Palaeolithic, and “Mode 1”, technologically-simple flake and core assemblages persist into the late Pleistocene and even in places the Holocene, even though the species of hominin that made them changed from *H. erectus* to *H. sapiens*. This is in sharp contrast to a region such as western Europe, where the shift from the Middle to Upper Palaeolithic was associated with the replacement of Neanderthals by *H. sapiens*, leaving aside a much-contested debate over the status of so-called “transitional industries” that could have been made by either. Changes in lithic technology in southern Asia are likely to have been more subtle, and discernible only through more rigorous quantitative analysis than merely noting the size and frequency of a few common elements.

1.1.3. DNA studies of modern populations do not detect extinct ones, or ones older than 60 ka

Analyses of the DNA of modern populations across southern Asia have made important contributions towards understanding the demographic history of *H. sapiens* outside Africa, and convincing arguments have been made that they first appeared in southern Asia ca 60 ka (Quintana-Murci et al., 1999; Macaulay et al., 2005; Soares et al., 2009). In China, similar studies indicate that the earliest populations of our species were present ca 50–60 ka (Su et al., 1999; Liu et al., 2006), or perhaps 27–56 ka (Zwiętkowice et al., 2003). However, these claims are based on studies of surviving extant populations, and cannot take into account those that became extinct during the last 60 ka. Additionally, coalescence ages from mitochondrial DNA and Y chromosome studies of contemporary Eurasian populations do not extend as far back as 125 ka, when *H. sapiens* first reached the Levant. By the same line of argument, any expansion of *H. sapiens* that might have occurred across southern Asia before 60 ka is currently undetectable through analyses of modern populations. This is particularly relevant to the Arabian Peninsula, which *H. sapiens* probably reached at the same time, or even perhaps earlier than, the Levant, as its presence there in MIS 5 is also undetectable through genetic analyses of modern populations (Cabrera et al., 2009). Moreover, given significant

environmental changes in Arabia over the course of the Late Pleistocene and Holocene, and the vulnerability of populations to even minor decreases in rainfall, we should anticipate that there were contractions and even local extinctions of hunter-gatherers, followed by population expansion and immigration from neighbouring regions. Thus the genetic make-up of contemporary populations in Arabia is likely only a partial – and recent – representation of the entire demographic history of the region, particularly because none has roots deeper than the late Pleistocene. Indeed, new genetic studies of Arabian populations indicate different source areas for indigenous peoples, with some groups representing much later Holocene expansions (Abu-Amero et al., 2008). The absence of any human skeletal evidence prior to the Holocene and the lack of ancient DNA studies continue to be major impediments to understanding the colonization and dispersal of populations of this critical region.

1.1.4. DNA studies of modern populations do not detect their residential histories

A point often overlooked in studies of the DNA of living populations is that they show their genetic, but not their residential history. As example, the Andaman Islanders are commonly regarded as the oldest surviving population in southern Asia, with a genetic history extending back 60 ka (Thangaraj et al., 2005), and this in turn has been used as evidence in favour of an early coastal dispersal of *H. sapiens* across southern Asia (Stringer, 2000; Field and Lahr, 2006). However, the fact that they have a genetic history extending back 60,000 years does not necessarily mean that they have inhabited the Andaman Islands, or have even been a coastal population, for that length of time. There is in fact no evidence that the islands were inhabited in the Pleistocene, as the earliest indications of occupation extend back only two millennia (Cooper, 2002). This might indicate that either the Pleistocene (and early Holocene) occupation of the islands has yet to be detected, or that the modern islanders were until recently living on the mainland, and not even necessarily on the coast for much of their history. The same point can be made about the 30-ka Denisova individual, known only from its ancient DNA: its origin is probably African (Krause et al., 2010) or Eurasian (Martínón-Torres et al., 2011), but its distribution and the point at which “Denisovans” first (or how often) inhabited Siberia remain unknown.

1.1.5. The timing of arrival of humans in Australia

A conservative estimate for the arrival of humans in Australia is ca 40 ka (O’Connell and Allen, 2004), when it was conjoined by lowered sea levels to New Guinea and Tasmania. This estimate is consistent with the date of the Niah cranium in Borneo, and the evidence from Timor, and with a narrative that envisages modern humans arriving in Southeast Asia ca 40 ka and shortly afterwards using boats or rafts with sails and paddles to colonise islands such as Timor and the Australian landmass. Recent evidence from New Guinea indicates that humans were already in the highlands by ca 49 ka, which would imply an earlier entry into Southeast Asia that preceded the earliest dates for Niah and Timor. If one accepts the earliest dates proposed by Roberts et al. (1994), humans reached Australia ca 60 ka. However, a recent genetic study of a 100-year old lock of Aboriginal hair implies that Aboriginal Australians are descended from a dispersal of *H. sapiens* into SE Asia ca 62–75 ka (Rasmussen et al., 2011). These uncertainties over the timing of arrival of humans in Australia have wider but unaddressed implications for the colonisation of southern Asia. An exit from Africa ca 60 ka and an arrival in Australia at 40 ka implies a slow rate of dispersal, and low rates of population increase in the donor population. In contrast, a near simultaneous departure from Africa and arrival in Australia implies an almost epidemic rate of population

growth in the donor region (presumably East African) and ensuing daughter populations, for which there is no evidence, and a dispersal event of *H. sapiens* as early as 62–75 ka into SE Asia implies that the date of dispersal from East Africa may have been under-estimated.

1.2. Emerging problems: donor regions, points of entry, and interbreeding

In addition to the above problems, three recent developments pose further difficulties for the existing model.

1.2.1. How many donor regions?

Emerging evidence from Northeast Africa indicates that the Jebel Irhoud (Morocco) cranium is that of *H. sapiens* rather than a Neanderthal, and is ca 160 ka old (Smith et al., 2007). Associated Middle Stone Age Aterian assemblages date back ca 145 ka at Ifri n’Anmaar. These include perforated beads from the Grotte des Pigeons (Morocco) that are ca 82 ka old, and thus predate the 75 ka old beads from Blombos, South Africa (Balter, 2011), which were previously the oldest known examples. Similar and even earlier examples are now known from Qafzeh, Israel, and Oued Djebbana, Algeria, where they are ca 100–135 ka (Vanhaeren et al., 2006). All this leads to the possibility not only that *H. sapiens* may have entered Southwest Asia from either North or East Africa, or both, but also that there may have been several dispersal events, involving different populations. As example, the 80 ka skull from Dar es-Soltan, Morocco, shows affinities with both those from Jebel Irhoud and Qafzeh (see Balter, 2011). Although these early populations of *H. sapiens* in Morocco may have been marginal to developments in Asia, the greening of the Sahara in the Last Interglacial and early part of the last glaciation (Drake et al., 2011) makes it more probable that they could have dispersed eastwards towards the Levant and Arabia during and after the Last Interglacial.

1.2.2. How many entry points from Africa into Asia?

Because the Levant is often envisaged as a crossroad that links Africa to Europe and continental Asia, it is frequently depicted as the principal entry point into Asia for the earliest anatomically modern humans that left Africa via the Sinai Peninsula or the Negev Desert at the north end of the Red Sea. This view is of course reinforced by the presence of *H. sapiens* in the northern Levant as early as 115–125 ka. It is not, however, the only route out of Africa, or even the most likely one (Derricourt, 2006). An alternative is the Bab al Mandab at the southern end of the Red Sea between the Horn of Africa and southern Yemen (Petraglia and Alsharekh, 2003), and 1200 miles south of the Sinai Peninsula. These straits are only 20 km wide, and at times of low sea level, perhaps only 12–15 km wide, and cannot be counted as a major sea barrier (Lambeck et al., 2011). With island hopping (especially at times of lowered sea levels), the distances across open water are reduced still further, although they were never totally eliminated (Rohling et al., 1998) (We should note also recent indications from Crete that humans – presumably *H. sapiens* – arrived there during the Last Interglacial after a sea-crossing of at least 70 km (Strasser et al., 2011)). A third route out of Africa that avoids the need to cross any open water is along the western and then eastern coasts of the Red Sea; after that, entry into the interior of the Arabian peninsula, where there were large river courses (Edgell, 2006) would have been relatively easy. Alternatively, hominins might have continued along the coast and dispersed along the coast of the Indian Ocean towards Oman, following lowered spring lines (Faure et al., 2002). There is no reason to exclude any of these routes; indeed it is likely that all were used, although not necessarily at the same time or by the same populations. Nevertheless, the Arabian Peninsula was

probably a more important faunal corridor than the Levant. Besides being geographically closer to East Africa than the Levant, the fauna of the Arabian Peninsula has few endemic mammalian species (only 10 out of 54, of which 7 are micro-mammals). Of the remaining 44 species (excluding bats), seven are shared with the Levant, and five with North Africa; eight are found from North Africa to Iran/Central Asia, nine are sub-Saharan (Ethiopian), three are Oriental, and 12 are cosmopolitan (Harrison and Bates, 1991). Its faunal history thus incorporates immigration and dispersal from several directions (and probably at different times), as does also its present-day human populations (Parker, 2009; Ridl et al., 2009). Irrespective of dispersal route(s), topographic and favourable environmental settings in Arabia (Parker, 2009) indicate that populations could have penetrated and expanded in these zones. If *H. sapiens* was present in the Levant for a period spanning 60 ka (from 130 to 70 ka), it seems inconceivable that similar populations were not also present in the well-watered and vegetated zones of Arabia at the same time.

1.2.3. The implications of ancient DNA (aDNA) studies

One of the most important revelations of the recent analysis of the aDNA of Neanderthal fossils is that they interbred with non-African modern humans before the divergence of modern Europeans, East Asians and Papuans, who thereby acquired ca 4–8% of their genes from Neanderthals (Green et al., 2010). This most likely occurred through contact in Southwest Asia between 100 and 125 ka (when *H. sapiens* is first recorded outside Africa) and 65 ka (when they became locally extinct in the Levant). Likewise, analysis of the aDNA of the Denisova individual also indicates inter-breeding with *H. sapiens*, hence the presence of some “Denisovan” genes in modern-day inhabitants in Melanesia, and the possibility that Denisovans once inhabited Southeast Asia (Reich et al., 2010). Both discoveries imply complex population histories in southern Asia, and the likelihood of hybridisation between Neanderthals, Denisovans and *H. sapiens*. By extension of the same reasoning, inter-breeding may also have occurred in East Asia between incoming populations of *H. sapiens*, and resident populations of *H. erectus*, whose genetic make-up remains unknown. This point has relevance to some of the specimens from South China, as indicated below.

1.3. Archaeological and human skeletal evidence

Recent evidence from Arabia, India, mainland and island Southeast Asia imply that the population history of southern Asia may have been more complex than envisaged under the current view, and that our species may have left Africa before 40–60 ka.

1.3.1. Arabia

Recent analysis indicates that some Arabian Middle Palaeolithic assemblages show affinities with both the Levant and East Africa. At Shi'bat Dihya in Southwest Yemen (opposite the Horn of Africa), assemblages with Levallois cores and tool forms date to ca 55 ka, and are said to be reminiscent of both the Levantine Mousterian and East African MSA, but are also idiosyncratic (Delagnes et al., in press; Macchiarelli, 2008). As mtDNA analysis indicates that *H. sapiens* was in southern Asia by 60 ka, it seems reasonably certain that any Middle Palaeolithic assemblage younger than that from southern Asia (including Arabia) would also have been made by *H. sapiens*, rather than Neanderthals. In contrast with Shi'bat Dihya, a lithic assemblage dated to ca 125 ka from Jebel Faya in Oman is claimed to have affinities with Northeast Africa, suggesting a population influx of *H. sapiens* from Northeast Africa during the Last Interglacial (Armitage et al., 2011) (Opinion remains sharply divided on this claim: Mellars, for example, states that “There’s not

a scrap of evidence here that these [tools] were made by modern humans, nor that they came from Africa” (see Lawler, 2011)). Nevertheless, given that so little is known about the early prehistory of the million-square miles of the Arabian Peninsula, we should not dismiss out of hand the possibility that modern humans were resident there before 60 ka, particularly because they were present scores of millennia before that date in the adjacent regions of Northeast Africa and Levant.

1.3.2. India

The crucial link between the western and eastern parts of southern Asia is India, which has traditionally played little part in discussions of modern human origins in Asia though this has been changing in recent years (James and Petraglia, 2005). In northern Pakistan, a small blade assemblage was excavated at site 55, Riwayat, and dated to ca 45 ka (Dennell et al., 1992) but most blade- and micro-blade dominated assemblages appear after ca 35 ka in peninsular India (Clarkson et al., 2009), given the caveat that there are more reliable dates available for sites such as Hayonim, Israel, than for the whole of India! Moreover, most radiocarbon and luminescence dates from India are single determinations, often made many years ago and long before laboratory and field techniques improved to their current standards.

Recent research in peninsular India has produced a great deal of new evidence that substantially revises previous knowledge of the Indian Palaeolithic sequence. Much of this new evidence has come about through intensive study of the Younger Toba Tuff (YTT) that resulted from the volcanic eruption of Toba in Sumatra ca 74 ka (Petraglia et al., 2007). As this was by far the largest eruption of the Pleistocene, a great deal of ash fell across India, and thus it provides a clear marker horizon (Petraglia et al., 2011). Most significantly, recent analyses of core reduction techniques show that these most resemble those of the African Middle Stone Age made by *H. sapiens*. Such assemblages can be distinguished from those made in the Levant by Neanderthals (Clarkson et al., 2011). This strongly implies that these Indian Middle Palaeolithic assemblages were also made by *H. sapiens*, and this suggestion further implies that it entered India earlier than the dates estimated from mtDNA data. Even more exciting is the recent discovery that stone assemblages from above and below the Toba ash are extremely similar technologically to those from early modern humans sites in sub-Saharan Africa, southeast Asia and Australia, suggesting modern humans may have entered India before the Toba eruption as part an early eastward dispersal from Africa (Clarkson et al., 2009; Petraglia et al., 2011). Although only a single find, the recovery of a tanged point under the Toba ash (Haslam et al., 2010), also suggests an African affiliation.

The earliest micro-blade industries excavated from rock shelters in India (Clarkson et al., 2009; Petraglia et al., 2009) and Sri Lanka (Deraniyagala, 1992; Perara et al., 2011) firmly date to ca 35 ka. Although it has been suggested that the tradition of making micro-blade tool forms and small crescentic tools was derived from the considerably older Howieson’s Poort assemblages from southern Africa, dated to ca 65–60 ka (Mellars, 2006), the most parsimonious explanation is that these are local innovations that may denote changes in hunting or plant processing activities, rather than the revival of a technique first initiated several thousands of kilometres distant and scores of millennia earlier. In support of this suggestion, there is currently no strong or convincing evidence for “Upper Palaeolithic” industries or symbolic assemblages, or microliths in early MIS 3 (i.e. >40 ka) or MIS 4 in either the Zagros (which is fairly well-documented for the last glaciation) or Arabia. If the micro-blade industries of the Indian subcontinent are local in origin, their wider significance is that *H. sapiens* did not arrive in southern Asia with a behavioural “package” of useful items and

techniques (e.g. microliths, bone points, fishing equipment), but developed these as and when they were locally useful (James, 2007), in the same way that has been proposed for Australia (Habgood and Franklin, 2008).

1.3.3. Southeast Asia

There are two slight hints that *H. sapiens* might have been present in island SE Asia and the Philippines before 50 ka. The first is a premolar from Punung, Java, dated on faunal grounds to 81–126 ka (Storm et al., 2005). Although identified as *H. sapiens*, Bacon et al. (2008) were not convinced that this constitutes convincing proof for the presence of modern humans in Java at such an early date. The second and stronger piece of evidence is a hominin 3rd metatarsal dated to ca 67 ka from Callao Cave, Luzon, the northern Philippines, that is described as not dissimilar to that of *H. sapiens*, *Homo habilis* and *Homo floresiensis* (Mijares et al., 2010). This find is especially intriguing as it is the first clear evidence of humans in the Philippines, apart from the late Pleistocene skeletal remains from Tabon, on Palawan Island off-shore from Borneo (see above), and indicates that humans (or other types of hominins) could make sea crossings before 65 ka. With the re-dating of the Ngandong *H. erectus* assemblage to the Middle Pleistocene (Indriati et al., 2011), there is now a gap of at least 100 ka between the most recent example of *H. erectus* and the earliest skeletal indication of *H. sapiens*.

1.3.4. South China

As most readers will be aware, most Chinese palaeo-anthropologists maintain that *H. erectus* evolved locally in East Asia into *H. sapiens*, with the early forms of our species best described as “archaic *H. sapiens*” (see e.g. Wu and Poirier, 1995).

This leads to an immediate confusion in that the same term is sometimes given to the earliest examples of *H. sapiens* in Africa. This point aside, there is still considerable uncertainty over the dating and context of these “archaic” specimens prior to 30 ka (see Bae, 2010). The main problems in evaluating the Chinese evidence (besides the obvious one over language for non-Chinese readers) are that excavations are not always fully published, some claims are based solely on isolated teeth, and there are doubts over the context and dating of finds, particularly in these complex cave environments (see Kaifu and Fujita, 2012). The hominin specimens from several cave sites are particularly problematic. At Liujiang, the breccias containing a cranium and post-cranial bones attributed to *H. sapiens* have been dated to a minimum age of 61–68 ka, but a probable age of 111–139 ka (Shen and Michel, 2007); they also suggest that the maximum age could be ≥ 153 ka. The layer containing *H. sapiens* teeth at Bailongdong cave was previously dated to 30–7 ka by ^{14}C , AMS and U–Th, but a stalagmite contemporary with the same layer has recently been dated to 160 ka (Shen et al., 2007). At Tubo Cave, stalagmites above and below a layer with human teeth were dated by Th–U to between 94 and 220 ka, and dating by ^{230}Th – ^{234}U and ^{227}Th – ^{230}U of two non-human teeth in the same layer to 85–139 ka (Shen et al., 2001). At Laibin, human teeth have been dated to a minimum of 39–44 ka, and a maximum of 112 ka (Shen et al., 2007). More recently, a mandible from Zhirendong, South China, has been attributed to *H. sapiens* and dated by U-series dating to ca 125 ka (Liu et al., 2010). Interestingly, because the mandible shows a mixture of characteristics associated with both *H. sapiens* and *H. erectus*, it is interpreted as showing interbreeding between the two species at an early date, rather than purely in situ evolution (An alternative interpretation is that it indicates a gracile late *H. erectus*; see Dennell, 2010).

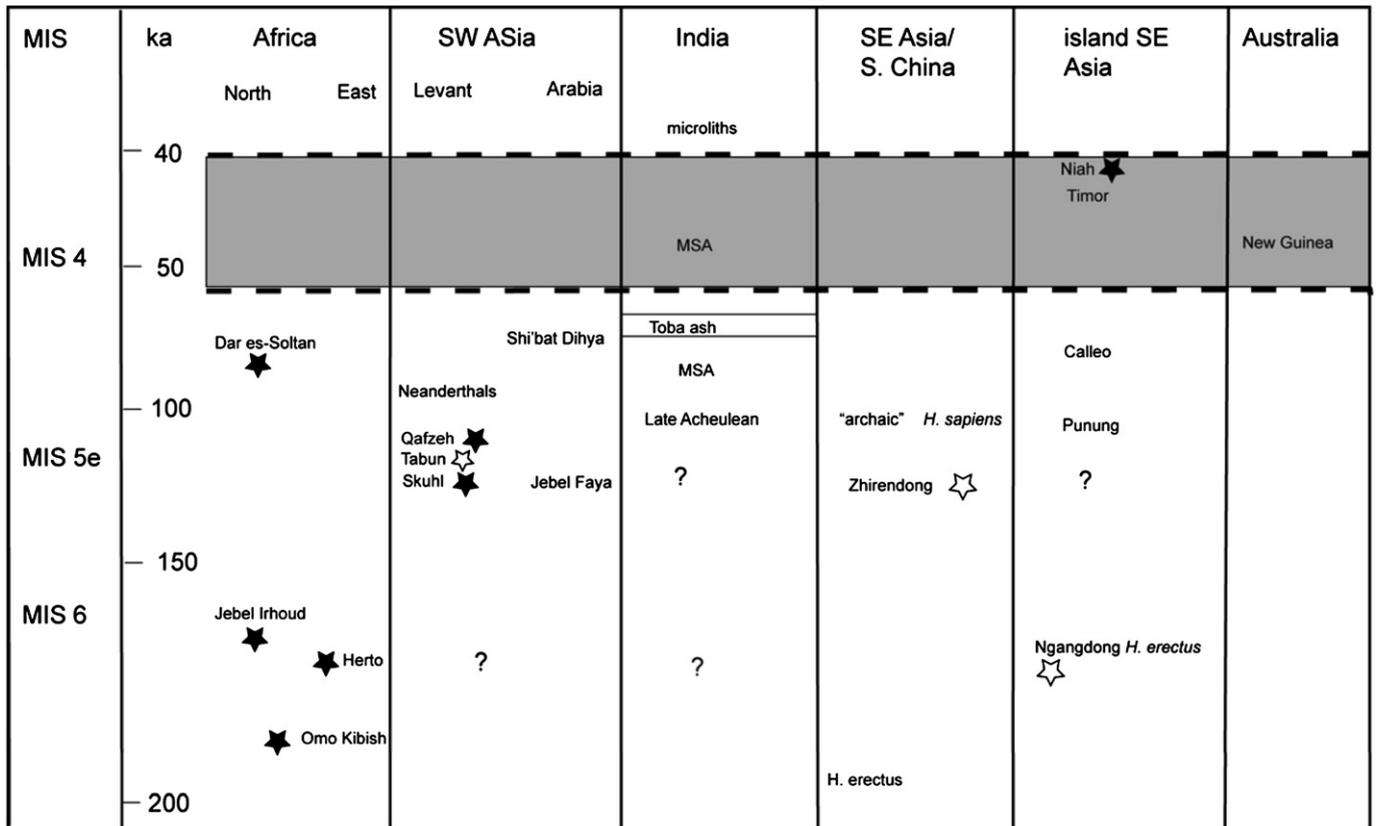


Fig. 1. A schematic summary of the dispersal of *H. sapiens* from SW Asia to Australia. The shaded area between 60 and 40 ka indicates the period during which *H. sapiens* is supposed to have dispersed across southern Asia. The scarcity of skeletal evidence across this region, particularly before 40 ka, allows other interpretations.

The Chinese evidence outlined above is clearly at odds with the conventional scenario for the colonisation of Southeast Asia by *H. sapiens*, with Niah as the earliest indication at ca 43 ka, and western scholars have tended to ignore these early dates, or reject them because of uncertainties over age and context. However, it might be advisable to consider alternative interpretations. As Kaifu and Fujita (2012: 8) suggest “a compatible scenario is that there was an earlier MIS 5 eastward dispersal of early modern humans but their genes did not significantly contribute to the genetic make-up of contemporary Asia people”. Because one implication of the aDNA evidence for both Neanderthals and “Denisovans” is that they interbred with *H. sapiens*, there is no a priori reason why *H. erectus* might not also have interbred with *H. sapiens* (and other extinct species), and produced off-spring with hybrid features (as suggested for Zhirendong). Additionally, if, as Reich et al. (2010) suggest, Denisovans inhabited Southeast Asia and interbred with *H. sapiens*, the population history of this region is likely much more complex than currently envisaged.

1.4. Discussion and implications

As with Out of Africa 1, the existing model of Out of Africa 2 has been a useful way of explaining a very small amount of information. Nevertheless, the present model unduly restricts the ways we can interpret the sparse, but recently much improved, data upon which it rests, and there are benefits to be gained from widening our range of possible hypotheses. A useful initial step would be for us to be more explicit about just how few reliable observations we have of early *H. sapiens* in southern Asia (Fig. 1); others would be to explore the likelihood that more than one donor population was involved in the earliest expansion of *H. sapiens* from Africa, that these expansions may have begun much earlier than currently envisaged, and dispersed via more than one entry point. As indicated above, there are good reasons for arguing that our species may have dispersed from Africa into Arabia and India earlier than previously thought, and therefore we should be open-ended as to how far east, and how early, they may have dispersed. Although movement out of Africa was likely restricted during the driest parts of MIS 6, there is no obvious reason why *H. sapiens* could not have entered Arabia during the Last Interglacial or during moist episodes during MIS 6, and perhaps migrated further east. Additionally, we have yet to develop models that accommodate the probability that early *H. sapiens* in Asia interbred with both Neanderthals and Denisovans. Here, it would help to move discussion beyond an either/or approach to Out of Africa or multi-regional models of modern human evolution, as both migration from Africa and inter-breeding with indigenous populations were likely involved, even if the role of each is impossible as yet to determine in most regions of southern Asia. Investigations of how, when, and how often *H. sapiens* dispersed across southern Asia need also to be integrated with environmental and climatic studies so that the responses of human (and other mammalian) populations to the changing conditions of MIS 3 and 4 (and perhaps earlier stages) can be properly assessed. We need to recognise that not all dispersal events are successful, and the first appearance of a species such as *H. sapiens* in a region does not necessarily indicate permanent colonisation. Under the challenging conditions of the Pleistocene, local contractions and even extinctions of populations are likely, just as with the Middle Pleistocene (see Dennell et al., 2011). In the same way that studies of Early and Middle Pleistocene hominin demography need to distinguish between short-term visitors and long-term residents (Dennell, 2003, 2009), so too do those of hominin dispersal in the Upper Pleistocene. Finally, discussions of the expansion of early *H. sapiens* from Africa need to be kept distinct from discussions of the diffusion of “modern behaviour”, however defined. Early *H. sapiens*

populations were emphatically not “modern” in the same senses as Holocene or Late Pleistocene ones (Klein, 2008), and the expansion of *H. sapiens* across southern Asia (and other regions) before 50 ka may have stemmed as much from ecological opportunism as from behavioural superiority over other hominin species.

Acknowledgements

We wish to thank Anne Delagnes, Mark White and Paul Pettitt for useful criticism and comment.

References

- Abu-Amero, K.K., Larruga, J.M., González, A.M., 2008. Mitochondrial DNA structure in the Arabian peninsula. *BMC Evolutionary Biology* 8, 45.
- Armitage, S.J., Jasim, S.A., Marks, A.E., Parker, A.G., Usik, V.I., Uerpmann, H.-P., 2011. The southern route “Out of Africa”: evidence for an early expansion of modern humans into Arabia. *Science* 331, 453–456.
- Athreya, S., 2007. Was *Homo heidelbergensis* in South Asia? A test using the Narmada fossil from central India. In: Petraglia, M.D., Allchin, B. (Eds.), *The Evolution and History of Human Populations in South Asia: Inter-disciplinary Studies in Archaeology, Biological Anthropology, Linguistics and Genetics*. Springer, Dordrecht, pp. 137–170.
- Bacon, Anne-Marie, Demeter, A.-M., Roussé, F., Vu The Long, S., Düringer, P., Antoine, P.-O., Thuy, Nguyen Kim, Mai, Bui Thi, Huong, Nguyen Thi Mai, Dodo, Y., Matsumura, H., Schuster, M., Anezaki, T., 2006. New palaeontological assemblage, sedimentological and chronological data from the Pleistocene Ma U’Oi cave (northern Vietnam). *Palaeogeography, Palaeoclimatology, Palaeoecology* 230, 280–298.
- Bacon, A.-M., Demeter, F., Düringer, P., Helm, C., Bano, M., Long, Vu The, Kim, Nguyen Thi, Antoine, P.-O., Mai, Bui Thi, Huong, Nguyen Thi Mai, Dodo, Y., Chabaux, F., Rihs, S., 2008. The Late Pleistocene Duoi U’Oi cave in northern Vietnam: palaeontology, sedimentology, taphonomy and palaeoenvironments. *Quaternary Science Reviews* 27, 1627–1654.
- Bae, C., 2010. The late Middle Pleistocene hominin fossil record of eastern Asia: synthesis and review. *American Journal of Physical Anthropology* 53, 75–93.
- Balter, M., 2011. Was North Africa the launch pad for modern human migrations? *Science* 331, 20–23.
- Barker, G.W.W., Barton, H., Bird, M., Daly, P., Datan, I., Dykes, A., Farr, L., Gilbertson, D., Harrison, 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, G., Stephens, M., Stringer, C., 2007. The ‘human revolution’ in lowland tropical Southeast Asia: the antiquity and behavior of anatomically modern humans at Niah Cave (Sarawak, Borneo). *Journal of Human Evolution* 52, 243–261.
- Bar-Yosef, O., Callander, J., 1999. The woman from Tabun: Garrod’s doubts in historical perspective. *Journal of Human Evolution* 37, 879–885.
- Bar-Yosef, O., 1988. Jordan prehistory: a view from the West. In: Henry, D.O. (Ed.), *The Prehistoric Archaeology of Jordan*. British Archaeological Reports (International Series), vol. 705, pp. 162–178.
- Cabrera, V.M., Abu-Amero, K.K., Larruga, J.M., González, A.M., 2009. The Arabian Peninsula: gate for human migrations out of Africa or cul-de-sac? A mitochondrial DNA phylogeographic perspective. In: Petraglia, M.D., Rose, J.I. (Eds.), *The Evolution of Human Populations in Arabia*. Springer, Dordrecht, pp. 79–87.
- 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.
- Clarkson, C., Jones, S., Harris, C., 2011. Continuity and change in the lithic industries of the Jurreru Valley, India, before and after the Toba eruption. *Quaternary International*.
- Cooper, Z., 2002. *Archaeology and History: Early Settlements in the Andaman Islands*. Oxford University Press, USA.
- Delagnes, A., Brenet, M., Crassard, R., Jaubert, J., Khalidi, L., Bertan, P., Macchiarelli, R., Mercier, N., Nomade, S., Peigné, S., Sítiz, L., Tournepeiche, J.-F., Tribolo, C. The Middle Paleolithic assemblage of Shi’bat Dihya 1 (Wadi Surdud site complex, Yemen). *Journal of Human Evolution*, in press.
- Demeter, F., Bacon, A.-M., Thuy, Nguyen Kim, Long, Vu The, Matsumura, H., Nga, Ha Huu, Schuster, M., Huong, Nguyen Mai, Coppens, Y., 2004. An archaic *Homo* molar from Northern Vietnam. *Current Anthropology* 45, 535–541.
- Demeter, F., Bacon, A.-M., Nguyen, Kim Thuy, Long, Vu The, Düringer, P., Rousse, S., Coppens, Y., Matsumura, H., Dodo, Y., Nguyen, Mai Huong, Tomoko, A., 2005. Discovery of a second human molar and cranium fragment in the late Middle to Late Pleistocene cave of Ma U’Oi (Northern Vietnam). *Journal of Human Evolution* 48, 393–402.
- Dennell, R.W., Roebroeks, W., 2005. An Asian perspective on early human dispersal from Africa. *Nature* 438, 1099–1104.
- Dennell, R., Rendell, H., Halim, M., Moth, E., 1992. A 45,000-year-old open-air Paleolithic site at Riwayat, northern Pakistan. *Journal of Field Archaeology* 19, 17–33.

- Dennell, R.W., Martínón-Torres, M., Bermudez de Castro, J.M., 2011. Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. *Quaternary Science Reviews* 30, 1511–1524.
- Dennell, R.W., 2003. Dispersal and colonisation, long and short chronologies: how continuous is the Early Pleistocene record for hominids outside East Africa? *Journal of Human Evolution* 45, 421–440.
- Dennell, R.W., 2009. *The Palaeolithic Settlement of Asia*. Cambridge Univ. Press, Cambridge.
- Dennell, R.W., 2010. Early *Homo sapiens* in China. *Nature* 468, 512–513.
- Deraniyagala, S.U., 1992. *The Prehistory of Sri Lanka: an Ecological Perspective*. Department of the Archaeological Survey, Government of Sri Lanka, Colombo.
- Derricourt, R., 2006. Getting “Out of Africa”: sea crossings, land crossings and culture in the hominin migrations. *Journal of World Prehistory* 19, 119–132.
- Détroit, F., Dizon, E., Falguères, C., Hameau, S., Ronquillo, W., Sémah, F., 2004. Upper Pleistocene *Homo sapiens* from the Tabon cave (Palawan, The Philippines): description and dating of new discoveries. *Comptes Rendus Palévol* 3, 705–712.
- Drake, N.A., Blench, R.M., Armitage, S.J., Bristow, C.S., White, K.H., 2011. Ancient watercourses and biogeography of the Sahara explain the peopling of the desert. *Proceedings of the National Academy of Sciences* 108, 458–462.
- Edgell, H.S., 2006. *Arabian Deserts. Nature, Origin and Evolution*. Springer, Dordrecht.
- Faure, H., Walter, R.C., Grant, D.R., 2002. The coastal oasis: ice age springs on emerged continental shelves. *Global and Planetary Change* 33, 47–56.
- Field, J.S., Lahr, M.M., 2006. Assessment of the southern dispersal: GIS based analyses of potential routes at Oxygen Isotope Stage 4. *Journal of World Prehistory* 19, 1–45.
- Forster, P., 2004. Ice ages and the mitochondrial DNA chronology of human dispersals: a review. *Philosophical Transactions of the Royal Society of London B* 359, 255–264.
- Frumkin, A., Bar-Yosef, O., Schwarcz, H.P., 2011. Possible paleohydrologic and paleoclimatic effects on hominin migration and occupation of the Levantine Middle Paleolithic. *Journal of Human Evolution* 60, 437–451.
- Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W., Fritz, M.H.-Y., Hansen, N.F., Durand, E.Y., Malaspina, A.-S., Jensen, J.D., Marques-Bonet, T., Alkan, C., Prüfer, K., Meyer, M., Burbano, H.A., Good, J.M., Schultz, R., Aximu-Petri, A., Butthof, A., Höber, B., Höffner, B., Siegemund, M., Weihmann, A., Nusbaum, C., Lander, E.S., Russ, C., Novod, N., Affourtit, J., Egholm, M., Verna, C., Rudan, P., Brajkovic, D., Kucan, Z., Gušić, I., Doronichev, V.B., Golovanova, L.V., Lalueza-Fox, C., de la Rasilla, M., Fortea, J., Rosas, A., Schmitz, R.W., Johnson, P.L.F., Eichler, E.E., Falush, D., Birney, E., Mullikin, J.C., Slatkin, M., Nielsen, R., Kelso, J., Lachmann, M., Reich, D., Pääbo, S., 2010. A draft sequence of Neandertal Genome. *Science* 328, 710–722.
- Grün, R., Stringer, C., 2000. Tabun revisited: revised ESR chronology and new ESR and U-series analyses of dental material from Tabun C1. *Journal of Human Evolution* 39, 601–612.
- Habgood, P.J., Franklin, N.R., 2008. The revolution that didn't arrive: a review of Pleistocene Sahul. *Journal of Human Evolution* 55, 187–222.
- Harrison, D.L., Bates, P.J.J., 1991. *Mammals of Arabia*, second ed. Harrison Zoological Museum, Sevenoaks.
- Haslam, M., Clarkson, C., Petraglia, M., Korisettar, R., Jones, S., Shipton, C., Ditchfield, P., Ambrose, S., 2010. The 74 ka Toba super-eruption and southern Indian hominins: archaeology, lithic technology and environments at Jwalapuram locality 3. *Journal of Archaeological Science* 37, 3370–3384.
- Howell, F.C., 1996. Thoughts on the study and interpretation of the human fossil record. In: Meikle, W.E., Howell, F.C., Jablonski, N.G. (Eds.), *Contemporary Issues in Human Evolution*. California Academy of Sciences Memoir 21, pp. 1–45.
- Indriati, E., Swisher, C.C., Lepre, C., Quinn, R.L., Suriyanto, R.A., Hascaryo, A.T., Grün, R., Feibel, C.S., Pobiner, B.L., Aubert, M., Lees, W., Antón, S.C., 2011. The age of the 20 meter Solo River Terrace, Java, Indonesia and the survival of *Homo erectus* in Asia. *PLoS One* 6, 1–10.
- James, H.V.A., Petraglia, M.D., 2005. Modern human origins and the evolution of behavior in the later Pleistocene record of South Asia. *Current Anthropology* 46, S3–S27.
- James, H.V.A., 2007. The emergence of modern human behavior in South Asia: a review of the current evidence and discussion of its possible implications. In: Petraglia, M.D., Allchin, B. (Eds.), *The Evolution and History of Human Populations in South Asia*. Springer, Dordrecht, pp. 201–227.
- Kaifu, Y., Fujita, M., 2012. Fossil record of early modern humans in East Asia. *Quaternary International* 248, 2–11.
- Klein, R.G., 2008. Out of Africa and the evolution of modern behaviour. *Evolutionary Anthropology* 17, 267–281.
- Klein, R., 2009. *The Human Career: Human Biological and Cultural Origins*, third ed. University Chicago Press, Chicago.
- Krause, J., Fu, Q., Good, J.M., Viola, B., Shunkov, M.V., Derevianko, A.P., Pääbo, S., 2010. The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. *Nature* 464, 894–897.
- Lambeck, K., Purcell, A., Flemming, N.C., Vita-Finzi, C., Alsharekh, A.M., Bailey, G., 2011. Sea level and shoreline reconstructions for the Red Sea: isostatic and tectonic considerations and implications for hominin migration out of Africa. *Quaternary Science Reviews* 30, 3542–3574.
- Lawler, A., 2011. Did modern humans travel out of Africa via Arabia? *Science* 331, 387.
- Liu, H., Prugnolle, F., Manica, A., Balloux, F., 2006. A geographically explicit genetic model of worldwide human-settlement history. *American Journal of Human Genetics* 79, 230–237.
- Liu, W., Jin, C.-Z., Zhang, Y.-Q., Cai, Y.-J., Xing, S., Wu, X.-J., Cheng, H., Edwards, R.L., Pan, W.-S., Qin, D.-G., An, Z.-S., Trinkhaus, E., Wu, X.-Z., 2010. Human remains from Zhirendong, South China, and modern human emergence in East Asia. *Proceedings of the National Academy of Sciences USA* 107, 19201–19206.
- Macaulay, V., Hill, C., Achilli, A., Rengo, C., Clarke, D., Meehan, W., Blackburn, J., Semino, O., Scozzari, R., Cruciani, F., Taha, A., Shaari, N.K., Raja, J.M., Ismail, P., Zainuddin, Z., Goodwin, W., Bulbeck, D., Bandelt, H.-J., Oppenheimer, S., Torroni, A., Richards, M., 2005. Single, rapid coastal settlement of Asia revealed by analysis of complete mitochondrial genomes. *Science* 308, 1034–1036.
- 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.
- Martínón-Torres, M., Dennell, R.W., Bermudez de Castro, J.M., 2011. The Denisova hominin need not be an African story. *Journal of Human Evolution* 60, 251–255.
- McDermott, F., Grun, R., Stringer, C.B., Hawkesworth, C.J., 1993. Mass spectrometric dates for Israeli Neanderthal/early modern sites. *Nature* 363, 252–255.
- McDougall, I., Brown, F.H., Fleagle, J.G., 2005. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature* 433, 733–736.
- Mellars, P., 2006. Going east: new genetic and archaeological perspectives on the modern human colonization of Eurasia. *Science* 313, 796–800.
- Mercier, N., Valladas, H., Froget, L., Joron, J.-L., Ronen, A., 2000. Datation par thermoluminescence de la base du gisement paléolithique de Tabun (mont Carmel, Israël). In: C. R. Académie de Science, Paris (ser. 2), vol. 330, 731–738.
- Mijares, A.S., Détroit, F., Piper, P., Grün, R., Bellwood, P., Aubert, M., Champion, G., Cuevas, N., De Leon, A., Dizon, E., 2010. New evidence for a 67,000-year-old human presence at Callao Cave, Luzon, Philippines. *Journal of Human Evolution* 59, 123–132.
- O'Connell, J.F., Allen, J., 2004. Dating the colonization of Sahul (Pleistocene Australia-New Guinea): a review of recent research. *Journal of Archaeological Science* 31, 835–853.
- O'Connor, S., 2007. New evidence from East Timor contributes to our understanding of earliest colonisation east of the Sunda Shelf. *Antiquity* 81, 523–535.
- Oppenheimer, S., 2011. A single southern exit of modern humans from Africa: before or after Toba? *Quaternary International*. doi:10.1016/j.quaint.2011.07.049.
- Parker, A.G., 2009. Pleistocene climate change in Arabia: developing a framework for hominin dispersal over the last 350 ka. In: Petraglia, M.D., Rose, J.I. (Eds.), *The Evolution of Human Populations in Arabia*. Springer, Dordrecht, pp. 39–49.
- Patnaik, R., Chauhan, P.R., Rao, M.R., Blackwell, B.A.B., Skinner, A.R., Sahni, A., Chauhan, M.S., Khan, H.S., 2009. New geochronological, palaeoclimatological and Palaeolithic data from the Narmada Valley hominin locality, central India. *Journal of Human Evolution* 56, 114–133.
- Perara, N., Kourampas, N., Simpson, I.A., Deraniyagala, S.U., Bulbeck, D., Kamminga, J., Perera, J., Fuller, D.Q., Szabo, K., Oliviera, N.V., 2011. People of the ancient rainforest: Late Pleistocene foragers at the Batadomba-lena rockshelter, Sri Lanka. *Journal of Human Evolution* 61, 254–269.
- Petraglia, M.D., Alsharekh, A., 2003. The Middle Palaeolithic of Arabia: implications for modern human origins, behaviour and dispersals. *Antiquity* 77, 671–684.
- Petraglia, M.D., Korisettar, R., Boivin, N., Clarkson, C., Ditchfield, P., Jones, S., Koshy, J., Lahr, M.M., Oppenheimer, S., Pyle, D., Roberts, R., Schwenninger, J.-L., Arnold, L., White, K., 2007. Middle Paleolithic assemblages from the Indian subcontinent before and after the Toba super-eruption. *Science* 317, 114–116.
- Petraglia, M., Clarkson, C., Boivin, N., Haslam, M., Korisettar, R., Chaubey, G., Ditchfield, P., Fuller, D., James, H., Jones, S., Kisivild, T., Koshy, J., Lahr, M.M., Metspalu, M., Roberts, R., Arnold, L., 2009. Population increase and environmental deterioration correspond with microlithic innovations in South Asia ca 35,000 years ago. *Proceedings of the National Academy of Sciences USA* 106, 12261–12267.
- Petraglia, M.D., Ditchfield, P., Jones, S., Korisettar, R., Pal, J.N., 2011. The Toba volcanic super-eruption, environmental change, and hominin occupation history in India over the last 140,000 years. *Quaternary International*. doi:10.1016/j.quaint.2011.07.042.
- Pettitt, P., 2005. *The rise of modern humans*. In: Scarre, C. (Ed.), *The Human Past*. Thames and Hudson, London, pp. 127–173.
- Quintana-Murci, L., Semino, O., Bandelt, H.-J., Passarino, G., McElreavey, K., Santachiara-Benerecetti, A.S., 1999. Genetic evidence of an early exit of *Homo sapiens* from Africa through eastern Africa. *Nature Genetics* 23, 437–441.
- Rasmussen, M., et al., (57 authors), 2011. An Aboriginal Australian genome reveals separate human dispersals into Asia. *Science* 334, 94–98.
- Reich, D., Green, R.E., Kircher, M., Krause, J., Patterson, N., Durand, E.Y., Viola, B., Briggs, A.W., Stenzel, U., Johnson, P.L.F., Maricic, T., Good, J.M., Marques-Bonet, T., Alkan, C., Fu, Q., Mallick, S., Li, H., Meyer, M., Eichler, E.E., Stoneking, M., Richards, M., Talmov, S., Shunkov, M.V., Derevianko, A.P., Hublin, J.-J., Kelsom, J., Slatkin, M., Pääbo, S., 2010. Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature* 468, 1053–1060.
- Ridl, J., Edens, C.M., Cerny, V., 2009. Mitochondrial DNA structure of Yemeni population: regional differences and the implications for different migratory contributions. In: Petraglia, M.D., Rose, J.I. (Eds.), *The Evolution of Human Populations in Arabia*. Springer, Dordrecht, pp. 69–78.
- Roberts, R.G., Jones, R., Spooner, N.A., Head, M.J., Murray, A.S., Smith, M.-A., 1994. The human colonisation of Australia: optical dates of 53,000 and 60,000 years bracket human arrival at Deaf Adder Gorge, Northern Territory. *Quaternary Geochronology (Quaternary Science Reviews)* 13, 575–583.
- Rohling, E.J., Fenton, M., Jorissen, F.J., Bertrand, P., Ganssen, G., Caulet, J.P., 1998. Magnitudes of sea-level lowstands of the past 500,000 years. *Nature* 394, 162–165.

- Schwarcz, H.P., Goldberg, P.D., Blackwell, B., 1980. Uranium series of dating of archeological sites in Israel. *Israel Journal of Earth Sciences* 29, 157–165.
- Schwartz, J.H., Tattersall, I., 2003. The Human Fossil Record. In: *Craniodental Morphology of Genus Homo (Africa and Asia)*, vol. 2. Wiley-Liss.
- Schwartz, J.H., Long, Vu The, Cuong, Nguyen Lan, Kha, Le Trung, Tattersall, I., 1995. A review of the Pleistocene hominoid fauna of the Socialist Republic of Vietnam (excluding Hylobatidae). *Anthropological Papers of the American Museum of Natural History* 76, 2–24.
- Shea, J.J., 2008. Transitions or turnovers? Climatically-forced extinctions of *Homo sapiens* and Neanderthals in the East Mediterranean Levant. *Quaternary Science Reviews* 27, 2253–2270.
- Shen, G., Michel, V., 2007. Chronological position of modern *Homo sapiens* sites in China based on U-series dating. *L'Anthropologie* 111, 157–165.
- Shen, G.J., Wang, W., Wang, Q., Pan, Y.J., 2001. U-series dating of hominid site Ganqian cave at Tubo, Liujiang Guangxi in South China. *Acta Anthropologica Sinica* 20, 238–244.
- Shen, G.J., Wang, W., Cheng, H., Edwards, R.L., 2007. Mass spectrometric U-series dating of Laibin hominid site in Guangxi, southern China. *Journal of Archaeological Science* 34, 2109–2114.
- Smith, T.A., Tafforeau, P., Reid, D.J., Grün, R., Eggers, S., Boukatiout, M., Hublin, J.-J., 2007. Earliest evidence of modern human life history in North African early *Homo sapiens*. *Proceedings of the National Academy of Sciences* 104, 6128–6133.
- Soares, P., Ermini, L., Thomson, N., Mormina, M., Rito, T., Röhl, A., Salas, A., Oppenheimer, S., Macaulay, V., Richards, M.B., 2009. Correcting for purifying selection: an improved human mitochondrial molecular clock. *American Journal of Human Genetics* 84, 740–759.
- Sohn, S., Wolpoff, M.H., 1993. Zuttiyeh face: a view from the East. *American Journal of Physical Anthropology* 91, 325–347.
- Stefan, V.H., Trinkhaus, E., 1998. Discrete trait and dental morphometric affinities of the Tabun C mandible. *Journal of Human Evolution* 34, 443–468.
- Storm, P., Aziz, F., Vos, J. de, Kosasih, D., Baskoro, S., Ngaliman, Hoek Ostende, L.W. van den, 2005. Late Pleistocene *Homo sapiens* in a tropical rainforest fauna in East Java. *Journal of Human Evolution* 49, 536–545.
- Storm, P., 2001. An environmental approach to the fate of *Homo erectus* in Australasia. In: Barham, L., Robson-Brown, K. (Eds.), *Human Roots: Africa and Asia in the Middle Pleistocene*. Western Academic and Specialist Press Ltd, Bristol, pp. 203–215.
- Strasser, T.F., Runnels, C., Wegmann, K., Panagopoulou, E., McCoy, F., Digregorio, C., Karkanas, P., Thompson, N., 2011. Dating Palaeolithic sites in southwestern Crete, Greece. *Journal of Quaternary Science*. ISSN: 0267-8179 ISSN: 0267-8179. doi:10.1002/jqs.1482.
- Stringer, C.B., 2000. Coasting out of Africa. *Nature* 405, 24–25.
- Su, B., Xiao, J., Underhill, P., Deka, R., Zhang, W., Akey, J., Huang, W., Shen, D., Lu, D., Luo, J., Chu, J., Tan, J., Shen, P., Davis, R., Cavalli-Sforza, L., Chakraborty, R., Xiong, M., Du, R., Oefner, P., Chen, Z., Jin, Li, 1999. Y-Chromosome evidence for a northward migration of modern humans into Eastern Asia during the last ice age. *American Journal of Human Genetics* 65, 1718–1724.
- Summerhayes, G.R., Leavesley, M., Fairbairn, A., Mandui, H., Field, J., Ford, A., Fullagar, R., 2010. Human adaptation and plant use in Highland New Guinea 49,000 to 44,000 years ago. *Science* 330, 78–81.
- Swisher III, C.C., Rink, W.J., Antón, S.C., Schwarcz, H.P., Curtis, G.H., Suprijo, A., Widiasmoro, 1996. Latest *Homo erectus* of Java: potential contemporaneity with *Homo sapiens* in Southeast Asia. *Science* 274, 1870–1874.
- Thangaraj, K., Chaubey, G., Kisivild, T., Reddy, A.G., Singh, V.K., Rasalkar, A.A., Singh, L., 2005. Reconstructing the origin of Andaman islanders. *Science* 308, 996.
- Tougaard, C., Jaeger, J.-J., Chaimanee, Yaowalak, Suteethorn, Varavudh, Triamwanchan, Somchai, 1998. Discovery of a *Homo* sp. tooth associated with a mammalian cave fauna of Late Middle Pleistocene age, Northern Thailand. *Journal of Human Evolution* 35, 47–54.
- Vanhaeren, M., d'Errico, F., Stringer, C., James, S.L., Todd, J.A., Mienis, H.K., 2006. Middle Paleolithic shell beads in Israel and Algeria. *Science* 312, 1785–1788.
- White, T.D., Asfaw, B., DeGusta, D., Gilbert, H., Richards, G.D., Suwa, G., Howell, F.C., 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423, 742–747.
- Wu, X., Poirier, F.E., 1995. *Human Evolution in China: a Metric Description of the Fossils and a Review of the Sites*. Oxford University Press, New York/Oxford.
- Zwiętkowice, E., Yotova, V., Gehl, D., Wambach, T., Arrieta, I., Batzer, M., Cole, D.E.C., Hechtman, P., Kaplan, F., Modiano, D., Moisan, J.-P., Michalski, R., Labuda, D., 2003. Haplotypes in the dystrophin DNA segment point to a mosaic origin of modern human diversity. *American Journal of Human Genetics* 73, 994–1015.