On the origin of modern humans: Asian perspectives

Christopher J. Bae, Katerina Douka, Michael D. Petraglia*

BACKGROUND: The earliest fossils of *Homo sapiens* are located in Africa and dated to the late Middle Pleistocene. At some point later, modern humans dispersed into Asia and reached the far-away locales of Europe, Australia, and eventually the Americas. Given that Neandertals, Denisovans, mid-Pleistocene *Homo*, and *H. floresiensis* were present in Asia before the appearance of modern humans, the timing and nature of the spread of modern humans across Eurasia continue to be subjects of intense debate. For instance, did modern humans replace the indigenous populations when moving into new regions? Alternatively, did population contact and interbreeding occur regularly? In terms of behavior, did technological innovations and symbolism facilitate dispersals of modern humans? For example, it is often assumed that only modern humans were capable of using watercraft and navigating to distant locations such as Australia and the Japanese archipelago—destinations that would not have been visible to the naked eye from the departure points, even during glacial stages when sea levels would have been much lower. Moreover, what role did major climatic fluctuations and environmental events (e.g., the Toba volcanic super-eruption) play in the dispersal of modern humans across Asia? Did extirpations of groups occur regularly, and did extinctions of populations take place? Questions such as these are paramount in understanding hominin evolution and Late Pleistocene Asian paleoanthropology.

ADVANCES: An increasing number of multidisciplinary field and laboratory projects focused on archaeological sites and fossil localities from different areas of Asia are producing important findings, allowing researchers to address key evolutionary questions that have long perplexed the field. For instance, technological advances have increased our ability to successfully collect ancient DNA from hominin fossils, providing proof that interbreeding occurred on a somewhat regular basis. New finds of *H. sapiens* fossils, with increasingly secure dating associations, are emerging in different areas of Asia, some seemingly from the first half of the Late Pleistocene. Cultural variability discerned from archaeological studies indicates that modern human behaviors did not simply spread across Asia in a time-transgressive pattern. This regional variation, which is particularly distinct in Southeast Asia, could be related at least in part to environmental and ecological variation (e.g., Palearctic versus Oriental biogeographic zones).

OUTLOOK: Recent findings from archaeology, hominin paleontology, geochronology, and genetics indicate that the strict “out of Africa” model, which posits that there was only a single dispersal into Eurasia at ~60,000 years ago, is in need of revision. In particular, a multiple-dispersal model, perhaps beginning at the advent of the Late Pleistocene, needs to be examined more closely. An increasingly robust record from Late Pleistocene Asian paleoanthropology is helping to build and establish new views about the origin and dispersal of modern humans.

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On the origin of modern humans: Asian perspectives

Christopher J. Bae,1* Katerina Douka,2,3* Michael D. Petraglia2,4*

The traditional “out of Africa” model, which posits a dispersal of modern Homo sapiens across Eurasia as a single wave at ~60,000 years ago and the subsequent replacement of all indigenous populations, is in need of revision. Recent discoveries from archaeology, hominin paleontology, geochronology, genetics, and paleoenvironmental studies have contributed to a better understanding of the Late Pleistocene record in Asia. Important findings highlighted here include growing evidence for multiple dispersals predating 60,000 years ago in regions such as southern and eastern Asia. Modern humans moving into Asia met Neandertals, Denisovans, mid-Pleistocene Homo, and possibly H. floresiensis, with some degree of interbreeding occurring. These early human dispersals, which left at least some genetic traces in modern populations, indicate that later replacements were not wholesale.

The origin of modern humans has long perplexed us. As the well-known paleanthropologist William Howells remarked more than four decades ago [(2), p. 477], “That part of human history covering the emergence of modern man and his regional differentiation continues to be surprisingly obscure. Locations of some elements of agreement or controversy...have long been clear, but the dimensions of the whole problem are far from obvious. The trees are familiar, but the forest is not.”

Perhaps the primary reason for this is that there has been no universal consensus on the traits that make us human. Arguments for a large cranial capacity defining our species went by the wayside with the realization that Neandertals, whose cranial capacity is slightly larger than ours on average, were not actually Cossack soldiers or pathological anomalies, but rather were of a much greater geological age than previously thought and in fact were penecontemporaneous with the earliest modern humans (2, 3). Further, we once assumed that “culture” clearly distinguished us from all other life forms. However, when Jane Goodall (4) returned from her field studies in the 1960s with the discovery that chimpanzees make and use tools, it raised questions about whether we could continue to use a broad variable such as culture to define humans.

The few generally agreed-upon autapomorphies specific to modern humans include such phenotypic traits as the presence of a mental eminence and a globular braincase. However, given the absence of the latter trait among the recently reported early modern human fossils from Jebel Irhoud, Morocco (5, 6), it may be possible that it developed much more recently, only within the past 130,000 years.

Some of the earliest morphologically modern humans are reported from the sites Omo Kibish, dating to ~195 thousand years ago (ka) (7), and Herto, dating to ~160 ka (8), both located in the Horn of Africa (Fig. 1A). These fossils have been used for the past several decades to support an East African origin for modern humans, corroborating similar findings from genetic studies (9-11). Yet the recent discovery of modern human fossils from Jebel Irhoud dating to ~310 ka (5, 12) raises important questions about the singular role of East Africa in the genesis of modern human morphology. Further, questions exist about whether so-called modern human behaviors appeared around the same time as modern human morphology, with most studies supporting a slower behavioral transition that occurred over the span of several hundred thousand years in Africa (13).

Despite the general acceptance that Homo sapiens arose in Africa, the initial arrival and survival of modern humans in different areas of the world continue to be strongly debated. Over the past several decades, Asia has been receiving increasing attention in these discussions, particularly because it is considered the conduit through which H. sapiens arrived in distant locales such as Western Europe, Australia, and eventually the Americas. Importantly, the Asian continent, bordered roughly by the Pacific, Indian, and Arctic Oceans on three sides and Europe to the west, includes a wide range of latitudinal, longitudinal, and even altitudinal variation, which has major implications for human evolution (14). Because the questions of what, where, how, and especially why with regard to our becoming “human” continue to be of great interest, we evaluate the debate on modern human origins and, specifically, how the Asian record contributes to addressing such questions.

The big questions

Findings from archaeology, hominin paleontology, geochronology, genetics, and paleoenvironmental studies have all been contributing to a better understanding of the Late Pleistocene human evolutionary record in Asia. Here we discuss some of the big questions that paleoanthropologists are investigating across Asia: Can modern human dispersal out of Africa be considered a single event occurring only after 60 ka, or is the picture more complicated? By which route(s) did modern humans disperse across Asia? What was the nature of the interactions between modern humans and hominin groups already present in Asia? What role did geographic and/or paleoenvironmental variations play in modern human dispersals?

Can the modern human dispersal be considered a single event occurring only after 60 ka?

Variations of the “out of Africa” (OoA) model may be broadly categorized as follows: (i) a single dispersal occurring during marine isotope stage (MIS) 5; (ii) multiple dispersals beginning during MIS 5; (iii) a single dispersal occurring during MIS 3; and (iv) multiple dispersals beginning during MIS 3. We detail each of these broadly defined models below, but we begin with the single-dispersal MIS 3 iteration because it has received the greatest attention, followed by the multiple-dispersal MIS 5 model.

Single dispersal during MIS 3

The traditional OoA model proposes that a single major dispersal event of modern humans out of Africa and into Eurasia occurred some time after 60 to 50 ka (15). In this model, earlier dispersals by anatomically modern humans into the Levant (e.g., Qafzeh and Skhul) were minor in scale and, for all intents and purposes, evolutionary dead ends. This OoA model was largely supported by early genetic studies and to various extents by archaeology, geochronology, and hominin paleontology (16–21). The 60-ka dispersal continues to be based primarily on genetic studies of present-day human population variation across the world. Given the degree of variability in the genetic clock (because of varying mutation rates and other uncertainties), it may be possible that this event occurred earlier or later than the 60-ka marker (18, 22). More recent whole-genome studies (23–25) suggest that a single major dispersal event occurred during which “all contemporary non-Africans branched off from a single ancestral population” [(26), p. 179] some time during the Late Pleistocene (27). Archaeologists have also set the boundary between 60 and 50 ka on the basis of the timing of the behavioral and technological transition from the Middle to the Upper Paleolithic (20, 21, 28).

Multiple dispersals during MIS 5

Another dispersal scenario that is receiving increasing attention is the possibility that multiple
dispersals began by the beginning of the Late Pleistocene \((34, 29–31)\). Given the increasing number of paleontological and archaeological reports of hominins from sites in different areas of Africa that supposedly predate 60 ka, it would appear that earlier dispersals out of Africa made it to the Levant (Qafzeh and Skhul) and probably also to South, East, and Southeast Asia (Fig. 1A and Table 1) \((32–42)\). At least some traces of these earlier dispersals would be expected to be present in the modern record. A recent genetic study seems to support the fossil and archaeological records in that ~2% of the genome of modern Papua New Guineans derives from an ancestry that predates the postulated 60-ka expansion by modern humans out of Africa \((43)\).

**Single dispersal during MIS 5 and multiple dispersals during MIS 3**

These two models receive the least support from the various scientific records. The model of a single dispersal during MIS 5 only works if modern humans suddenly appeared all across Asia in large numbers and remained so continuously throughout the Late Pleistocene. Although a growing number of sites have been dated to MIS 5 and 4, and a number of these are considered to be associated with modern humans, the data do not seem to reflect a major dispersal event at this early date (compare Fig. 1, A and B). No genetic studies of which we are aware support such a model. The model of multiple dispersals during MIS 3 only works if there is no evidence for modern humans before MIS 3 (compare with Fig. 1A).

**By which route(s) did modern humans disperse across Asia?**

The most widely discussed OOA routes have East Africa as the departure point into Asia. Researchers have hypothesized two distinct paths: The first involves crossing over from northern Egypt to the Sinai Peninsula, whereas the second involves crossing the Bab al Mandab Strait to Yemen in the southernmost part of the Arabian Peninsula \((30, 44–46)\) (Fig. 1A). The Bab al Mandab Strait is usually about 20 km wide, and during glacial periods, it may have only been about 5 to 15 km wide. Given the short distances involved, the other continent would have been visible from the points of both departure and arrival \((47)\), as is the case today. Yet this route requires a water crossing that would have made rafting a necessity. The Sinai Peninsula, on the other hand, is the only land corridor that has persisted since the permanent closing of the Tethys Seaway during the Miocene. This land route remains the strongest, and, for some, the most parsimonious candidate for the key dispersal pathway beyond Africa \((48, 49)\).

There is little consensus as to the route(s) taken once outside of Africa. Two major directional dispersal models have been proposed: northern and southern. The northern dispersal model posits that humans moved north of the Sinai and through the Negev region to reach the eastern Mediterranean Levant \((48)\). Evidence to support this includes the early modern human sites of Skhul and Qafzeh in Israel that date to between 120 and 90 ka and proposed technological similarities between artifact assemblages in northeastern Africa and the Levant \((44, 48, 50, 51)\). After this period, there is no evidence for the presence of modern humans in the Levant until about 55 ka or later, based on the recent findings from Manot Cave \((52)\). Because of this paucity of evidence, the early presence of modern humans in the Levant is considered by many to be a failed dispersal event.

The basic tenet of the southern dispersal hypothesis is an eastward expansion from the Horn of Africa via the Strait of Bab al Mandab, across the southern part of the Arabian Peninsula, along the Yemen-Oman littorals to the Persian Gulf, and then along the coast of the Indian subcontinent \((18)\). Upon arrival at the Sunda shelf, and after a short hiatus, humans dispersed to Sahul, eventually reaching Australasia soon after 60 ka \((53)\). The southern coastal dispersal route out of Africa and around the Indian Ocean continues to receive substantial attention, in part because a number of genetic studies seem to support it \((e.g., 48, 19, 25)\). However, for modern humans to have been able to traverse the southern coastal route, regular access to fresh water and utilization of marine resources would have been necessary \((54, 55)\). Unfortunately, clear evidence for a coastal dispersal around the Indian Ocean is not present for regions outside Sunda, and instead, dispersal from the Sinai across terrestrial regions of Arabia and southern Asia is surmised as the main route of population movements \((29–31)\). It is possible that although coastlines provided favorable habitats, at least occasionally, reliance on such resources should be seen as only one component of the whole human subsistence package \((31)\).

**FADs and FAQs**

An important point in developing a more concrete understanding of the timing and direction of human movements outside Africa is that the first appearance datum (FAD) of modern humans can serve as terminus ante quem (TAQ) for when these dispersals began. In this regard, with the emphasis on the supposed “end points,” the key arrival areas are Europe, Australasia, the Japanese archipelago, and eventually the New World. Europe has long been at the forefront of these migrations as the key dispersal point for Homo sapiens, based on evidence from the most important sites dated to between 60 and 30 ka. Yellow stripes and translucent orange represent tentative ranges for Neandertals and early Homo sapiens, respectively.
discussions because it is a heavily studied region and an area that was occupied by Neandertals for several hundred thousand years, with only about a 5000- to 3000-year overlap with modern humans after initial colonization by the latter group (60). Although migration corridors between Europe and the Levant may have been present during MIS 5 (57), evidence for an unequivocal FAD by modern humans before 44 ka is absent. The earliest example of fully modern human anatomy in Europe is the mandibular fragment from Kent’s Cavern in England and the Cavallo teeth from southern Italy (58, 59), dating to between 41 and 44 ka (Fig. 1B). However, given the geographic location of both sites, and assuming that dispersals into Europe originated from the Levant or elsewhere in northern Asia and traveled westward, this opens the possibility that earlier evidence for modern humans in central or eastern Europe may be present.

It has long been argued that modern humans were the only hominin taxon capable of peopling Australasia, particularly because it would have involved the ability to build sturdy watercraft and navigate the open seas (60). The peopling of Australasia took on greater importance once it was realized that it likely occurred some time between 60 and 40 ka (61, 62). The recent re-analysis of the Madjedbebe (Malakunanja II) site in northern Australia pushes the initial peopling of the region back to at least 59 ka and possibly 65 ka (63), although no fossils have been recovered from the site. With early modern human fossils being reported in mainland Southeast Asia (36, 39, 40), Indonesia (42), and the Philippines (38) (Fig. 1A) that predate the findings from Madjedbebe (65 ka) and New Guinea (49 ka (64)), this is perhaps not all that surprising.

A major colonization event that has not received as much attention is the peopling of the Japanese archipelago; it has been suggested that this could have occurred during MIS 6, when a land connection was likely present, or some time during MIS 3, when no land connection existed (28, 65–67). Given that only a few sites in Japan predate 40 ka, and that there are questions about the context and/or artificial nature of the materials at those localities, the earliest presence of modern humans in Japan is considered to be about 40 ka (67). Assuming that this date is correct, the initial colonization would have had to involve some type of watercraft and a high degree of seafaring skill (28, 34, 65, 66).

The timing and route by which humans arrived in the Americas have been the subjects of a long and often heated debate (68, 69). Most data appear to support colonization through Beringia either via the ice corridor or the coastal route some time during or right after the last glacial maximum (~20 to 15 ka) (68). However, to reach North America, human foragers had to have first arrived in Siberia. The earliest peopling of Siberia north of 50°N appears to have only occurred some time between 50 and 45 ka, as indicated by the human femur from Ust’-Ishim in western Siberia (70), and the earliest peopling north of 60°N occurred perhaps only as recently as 32 ka (68, 71). Neandertals and Denisovans were clearly in southern Siberia during the first half of the Late Pleistocene, but more northward dispersals were likely by modern humans (Fig. 1B).

**How did modern humans interact with hominin groups already present in Asia?**

When humans arrive in a new territory, one of several things may happen, generally ranging from admixture and the sharing of culture to competition between and possibly the extinction of one of the populations (45). Data from genetics and archaeology have directly contributed to increasing our understanding of what may have happened when Late Pleistocene humans moved into new regions of Asia.

**Introgression**

Over the past decade, technological advances in the field of ancient DNA analysis have allowed scientists to obtain uncontaminated genomewide data from Pleistocene hominin fossils. This has shown that a fair degree of introgression occurred between Neandertals and modern humans (27, 72–74). In fact, estimates of Neanderthal DNA present in non-African modern humans generally range between 1 and 4% (72). One estimate from the Romanian Pestera cu Oase 1 fossil is as high as 9%, suggesting that this particular modern human with a minimum age of 40,000 years may have had a Neandertal ancestor as recently as four to six generations back (75). The recent genetic identification of penecontemporaneous Denisovans in southern Siberia further complicates the Late Pleistocene human evolutionary picture in Asia (76–78). Reich and colleagues (80) estimated that about 5% of modern-day Melanesian DNA originates from this ancestral Denisovan population, although more recent estimates are between 1 and 3% (27, 81). Further, Prüfer and colleagues (73) found that Neandertals, who were also present at Denisova Cave, interbred with Denisovians; similarly, gene flow occurred between Denisovians and a yet-to-be-identified hominin population. In the latter case, Prüfer and colleagues (73) postulated that the gene flow could be from an ancestral population, such as *H. erectus*. Thus, a

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**Table 1. Background data for all Asian Late Pleistocene sites associated with early modern humans that appear in Fig. 1A.** Triple plus signs indicate high confidence (hominin fossils and archaeology found in clear association with solid dates); double plus signs, medium confidence (hominin fossils and/or archaeology found in association or questionable association with dates); single plus sign, weak confidence (hominin fossils and/or archaeology found in questionable association with dates).

<table>
<thead>
<tr>
<th>Site number in Fig. 1A</th>
<th>Site</th>
<th>Present-day country</th>
<th>Proposed age range (thousand years)</th>
<th>Hominin fossils</th>
<th>Archaeology</th>
<th>Confidence</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>Skhul, Qafzeh</td>
<td>Israel</td>
<td>120 to 90</td>
<td>Yes (H. sapiens)</td>
<td>Yes</td>
<td>+++</td>
<td>(50, 51)</td>
</tr>
<tr>
<td>10</td>
<td>Jebel Qattar</td>
<td>Saudi Arabia</td>
<td>75</td>
<td>None reported</td>
<td>Yes</td>
<td>++</td>
<td>(110)</td>
</tr>
<tr>
<td>11</td>
<td>Mundafan</td>
<td>Saudi Arabia</td>
<td>100 to 80</td>
<td>None reported</td>
<td>Yes</td>
<td>++</td>
<td>(31)</td>
</tr>
<tr>
<td>12</td>
<td>Aybut Al Auwal</td>
<td>Oman</td>
<td>105</td>
<td>None reported</td>
<td>Yes</td>
<td>++</td>
<td>(111)</td>
</tr>
<tr>
<td>13</td>
<td>Jebel Faya C</td>
<td>United Arab Emirates</td>
<td>125</td>
<td>None reported</td>
<td>Yes</td>
<td>++</td>
<td>(112)</td>
</tr>
<tr>
<td>14</td>
<td>Katoi, 16R Dune</td>
<td>India</td>
<td>96, 80</td>
<td>None reported</td>
<td>Yes</td>
<td>++</td>
<td>(95)</td>
</tr>
<tr>
<td>15</td>
<td>Jwalapuram</td>
<td>India</td>
<td>85 to 75</td>
<td>None reported</td>
<td>Yes</td>
<td>++</td>
<td>(33)</td>
</tr>
<tr>
<td>16</td>
<td>Huanglong</td>
<td>China</td>
<td>100 to 80</td>
<td>Yes (H. sapiens)</td>
<td>Yes</td>
<td>++</td>
<td>(35)</td>
</tr>
<tr>
<td>17</td>
<td>Luna</td>
<td>China</td>
<td>120 to 70</td>
<td>Yes (H. sapiens)</td>
<td>Yes</td>
<td>++</td>
<td>(40)</td>
</tr>
<tr>
<td>18</td>
<td>Lijujiang</td>
<td>China</td>
<td>130 to 70</td>
<td>Yes (H. sapiens)</td>
<td>None reported</td>
<td>+</td>
<td>(32)</td>
</tr>
<tr>
<td>19</td>
<td>Fuyan</td>
<td>China</td>
<td>120 to 80</td>
<td>Yes (H. sapiens)</td>
<td>None reported</td>
<td>++</td>
<td>(37, 41)</td>
</tr>
<tr>
<td>20</td>
<td>Ziren</td>
<td>China</td>
<td>100</td>
<td>Yes (H. sapiens)</td>
<td>None reported</td>
<td>++</td>
<td>(36)</td>
</tr>
<tr>
<td>21</td>
<td>Tam Pa Ling</td>
<td>Laos</td>
<td>63 to 46</td>
<td>Yes (H. sapiens)</td>
<td>None reported</td>
<td>++</td>
<td>(39)</td>
</tr>
<tr>
<td>22</td>
<td>Callao</td>
<td>Philippines</td>
<td>67</td>
<td>Yes (H. sapiens?)</td>
<td>Yes</td>
<td>++</td>
<td>(38)</td>
</tr>
<tr>
<td>23</td>
<td>Lida Ajer</td>
<td>Sumatra</td>
<td>73 to 63</td>
<td>Yes (H. sapiens)</td>
<td>Yes</td>
<td>++</td>
<td>(42)</td>
</tr>
<tr>
<td>24</td>
<td>Madjedbebe</td>
<td>Australia</td>
<td>65</td>
<td>None reported</td>
<td>Yes</td>
<td>++</td>
<td>(63)</td>
</tr>
</tbody>
</table>
The growing number of studies indicate multiple admixture events between modern humans, Neandertals, Denisovans, and a nonidentified population—events assumed to have occurred in Asia (11, 73, 82). Substantial overlap in time ranges in these same areas also lends support to likely interactions between these different populations (Fig. 2).

Genetic studies have shown that the admixture between non-African modern humans and Neandertals could have occurred as recently as 40 to 86 ka (70, 75). The younger date would tend to support the 60-ka OOA model, whereas the older admixture date could be interpreted as one of the early dispersals thought to have occurred during MIS 5. Malaspinas and colleagues (23) presented an even more complex admixture model and suggested a series of events that occurred between 72 and 42 ka, which included a “ghost” lineage. To further complicate the matter, Posth and colleagues (74) recently suggested that the beginning of H. sapiens–Neandertal introgression could date to as far back as ~270 ka.

Although indications of introgression now commonly appear in the genetic literature, we should attempt to determine whether it is possible to identify how genetic interchange appears phenotypically. A range of studies of hybrids among closely related nonhuman primates identified examples of dysgenesis (“hybrid weakness”) and/or heterosis (“hybrid vigor”) when evaluating a diversity of size and shape variables (83). A number of fossils have been proposed as possible hybrids in the Late Pleistocene human fossil record (84), including from Pesteru șu Oase in Romania (85) and Zhirendong in China (36). Martínón-Torres and colleagues (86) even recently suggested that H. floresiensis may be a hybrid. The key to phenotypically identifying a hybrid may be to observe, with some regularity, unusual traits (e.g., supernumerary teeth) that are not present in the proposed parent population but suddenly appear in the supposed offspring.

**Cultural diffusion**

In a straightforward scenario, modern humans would have moved out of Africa and into Asia carrying with them a set of standard “modern” behaviors (e.g., the use of blades, microblades, art, and symbolism). This is commonly referred to as the “human revolution” model, thought to reflect the Middle to Late Paleolithic transition (21, 28, 55). Numerous studies, however, have questioned whether a behavioral revolution actually took place and whether a model, originally developed for the western European record, is suitable to other regions of the Old World (e.g., 13, 34, 87–90). Further, the human behavioral and skeletal records do not line up neatly: Modern human behaviors often appear in areas where modern human fossils do not. Behaviors traditionally considered to be representative of modern humans now have been reported in association with Neandertals, Denisovans, and possibly other hominin taxa (91–93).

Blade technology, long considered one of the core components of the Upper Paleolithic in Asia, appeared in western Asia after 50 ka and arrived in South and North Asia sometime afterward. Microblades appeared during early MIS 3 in South Asia and late MIS 3 in North Asia, becoming more prominent after 35 and 25 ka, respectively (31, 33, 34, 94, 95). Interestingly, early blade and microblade technologies have yet to be identified in Southeast Asia, including southern China. Because Southeast Asia represents a different biogeographic zone (Oriental) than the other regions (Palaearctic), this suggests that different ecological demands required the development of a different behavioral toolkit to survive (14, 34, 96–98). Early evidence of rock art (99) and deep-sea pelagic fishing (100) in Southeast Asia are clear signs of other forms of modern human adaptation.

It has long been thought that modern human foraging groups moving over the northern route through Asia carried with them a modern behavioral package (28, 34, 101), sometimes equated with the Initial Upper Paleolithic technocomplex. Interestingly, however, the recent identifications of Denisovans and Neandertals in Denisova Cave—a site that has traditionally been known for the presence of a diverse Upper Paleolithic industry (e.g., blades, bone tools, and bone ornaments) (102)—has complicated this dispersal model, particularly given the apparent absence of H. sapiens fossils at the site (Box 1). A set of perforated teeth and ostrich eggshell and bone pendants were excavated from layer II of Denisova Cave, the same layer that is assigned to Neandertals (sublayer 11.4) and Denisovans (sublayer 11.2) (73). This may add to the growing evidence that, at least on a small scale, Neandertals and perhaps other hominins were capable of symbolic behavior (91, 92). Alternatively, we may be witnessing a series of local extinction and/or

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**Fig. 2. Age ranges for the presence of different hominin taxa (modern humans, Neandertals, Denisovans, and H. floresiensis) in all major regions of Asia.** The dotted line represents the proposed 60-ka exodus out of Africa supported by various studies. If the 60-ka model is correct, modern humans should not appear in Asia earlier than that. NGRIP, North Greenland Ice Core Project.
Box 1. Who were the Denisovans?

On the basis of DNA sequencing of a juvenile finger bone found almost a decade ago, a previously unknown Late Pleistocene hominin population was identified from Denisova Cave in the Altai Mountains in southern Siberia, now referred to as the Denisovans (76, 77). The hominin fossil assemblage from Denisova Cave includes this distal manual phalanx from layer 11.2 (Denisova 3) and an upper left M3 or M2 tooth from layer 11.1 (Denisova 4), found in association with various archaeological materials typical of both the late Middle Paleolithic (e.g., Levallois flakes) and the Upper Paleolithic (e.g., microblades and ornamentals made from ground stone) (112). In addition, an upper molar (Denisova 6) was found at the interface of layers 11.4 and 12 in 2010, tentatively also identified as an M3 or M2 (78), and a lower left molar (Denisova 2) was recently added to the small number of fossils from the site (79). The archaeological sequence begins at about 250 ka; Denisova 8 has been tentatively dated to >50 ka, whereas Denisova 3 and 4 have been dated to between 50 and 30 ka (76–78), although it is likely that these dates will be revised after further geochronological study.

Despite the fact that genetic analyses indicated that the Denisovans were statistically significantly different from both modern humans and Neandertals, comparative morphological studies of the phalanx and molars were inconclusive (11, 77, 78). Thus, these remains were referred to simply as Denisovans and not assigned a new species name. Since these initial studies, however, suggestions have arisen that Denisovans may be present in the fossils of Chinese mid-Pleistocene Homo (or even Penghu 1 from Taiwan) (44, 86, 114). Initial comparative studies have shown that the Denisovan dentition displays similarities with those of the Chinese Xujiayao hominin fossils and Teshik-Tash and Oase 2 fossils from western Asia (115, 116). To further complicate matters, at least three Neandertal fossils were also identified at the site (Denisova 5, 9, and 11) (73, 117).

What role did geographic and/or paleoenvironmental variations play?

Modern humans dispersing out of Africa and into Asia were able to adjust to a diversity of paleoenvironmental variations play? What role did geographic and/or the present-day submergence of coastlines containing traces of hominin occupation will hinder reconstruction of dispersal routes, particularly during major glacial periods when sea levels were ~100 m below their current levels (54). A good example of this is the eastern China seaboard: During glacial periods, the coastal plain would have extended outward 400 to 600 km and connected areas such as the Shandong Peninsula in eastern China with the Korean Peninsula, facilitating movement of a variety of animals, including humans, across the dry Yellow Sea (94). In the Korea-China case, there is good reason to assume that a number of archaeological sites and Pleistocene faunas are present in this submerged former coastal plain. It is not clear that the same argument can be made for all coastal regions in Asia. For instance, proponents of the southern coastal dispersal model argue that the reason that there is a paucity of evidence of coastal occupation is that the sites are now submerged (77, 53). However, the coastline along the Indian Ocean rim and the western side of the Sunda Shelf has areas of relatively steep drop-off, so that it is unlikely that many coastal sites would be now submerged; moreover, archaeological surveys in these steep coastal shelves and in some uplifted shoreline areas have failed to find Late Pleistocene coastal sites (31).

So what happened then?

Growing evidence indicates that modern human dispersals out of Africa into Asia occurred by 60 ka and afterward (Fig. 1B). Such dispersal events across Eurasia are supported by a diversity of studies from genetics and archaeology (11, 20, 28). However, increasing findings indicate that multiple dispersals out of Africa by early modern humans began during MIS 5, resulting in their earlier arrival in distant localities in the Levant, South Asia, Southeast Asia, and China (33, 35–37, 39–42, 50) (Fig. 1A).

The initial dispersals out of Africa during MIS 5 were likely by small groups of foragers, and these appear to have moved along both a southern and a northern route. The initial dispersal by modern humans northward reached at least Qafzeh and Skhul. The southern route may have followed the coast around the Indian Ocean (18–20), but archaeological evidence dominates for inland dispersal corridors, where a diversity of habitats occur and where reliable freshwater rivers, lakes, and animal resources were present (29–31). Sites dating to early MIS 5 to MIS 4 that appear in places such as India, southern China, Laos, Sumatra, and the Philippines are all located a fair distance from any paleocoasts. At least some of these early dispersals left low-level genetic traces in modern human populations (43).

A later, major OoA event most likely occurred some time around 60 ka and thereafter. This later dispersal by larger and more demographically successful human populations masked genetic traces of the earlier dispersals (73). These dispersals across Asia occurred in both northerly and southerly directions (28). In the move north, modern human foragers skirted the Qinghai-Tibetan Plateau to its south to eventually reach Siberia (70). At around the same time or soon after, populations reached Europe. These northward-traveling human populations carried an advanced toolkit comprising microliths, blades, composite tools, and symbolic objects (beads and colorants), which eventually facilitated their dispersal and successful establishment in higher latitudes and altitudes. These foraging groups carrying a specialized microblade toolkit eventually made their way to the Americas through Beringia (69). The southern route includes possible movement pathways through the Indian subcontinent, mainland Southeast Asia, and eventually as far north as central China and southward into the Southeast Asian islands and on to Australasia. Questions remain as to why modern human foragers arriving in Southeast Asia discarded blade and microblade stone tool industries, although evidence indicates that communities had ground stone technologies, which represented adaptations to new environments (67). Further, there are questions concerning what happened when different foraging groups, originating in areas to the north and south, met in central China (34, 89).

Moving forward: Future directions of Late Pleistocene Asian paleoanthropology

A rigid definition of the OoA model positing that modern humans dispersed from Africa only after 60 ka and simply replaced all indigenous populations (e.g., mid-Pleistocene Homo, Neandertals, Denisovans, and H. floresiensis) with no interbreeding can no longer be considered valid. What is needed now is to develop more detailed

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models that include the growing evidence for early dispersals, contractions, extinctions, and extinctions of human groups and lineages, while recognizing that not all pre–60 ka dispersals were evolutionary dead ends. Further, there are still large swathes of territory in Asia that remain largely unexplored, and previously identified sites and materials are in need of renewed study. Fortunately, the increasing number of multidisciplinary research programs launched in Asia over the past few decades has resulted not only in the reporting of many important sites and findings, but also the accumulation of information that fills in gaps in the evolutionary record, thereby facilitating broader interregional comparisons.

As attested by the great interest generated by the Central Asiatic Expeditions in the early 20th century, Asia was once considered to be the cradle of mankind (74). Although important finds from Europe and Africa over the course of the past century have diverted attention, Asia is a continent that has much to offer to research on modern human origins, thereby shaping what we think about our evolution and history.

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14. V. Macaulay, New insights into the Neolithic of Europe and Africa over the course of the past century have diverted attention, Asia is a continent that has much to offer to research on modern human origins, thereby shaping what we think about our evolution and history.

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On the origin of modern humans: Asian perspectives
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The peopling of Asia
In recent years, there has been increasing focus on the paleoanthropology of Asia, particularly the migration patterns of early modern humans as they spread out of Africa. Bae et al. review the current state of the Late Pleistocene Asian human evolutionary record from archaeology, hominin paleontology, geochronology, genetics, and paleoclimatology. They evaluate single versus multiple dispersal models and southern versus the northern dispersal routes across the Asian continent. They also review behavioral and environmental variability and how these may have affected modern human dispersals and interactions with indigenous populations.

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